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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 84, NO. 2, PP. 69–78 MARCH, 1957

ZONATION AND ORGANIZATION OF ROOT APICAL MERISTEM OF GLYCINE MAX[1]

C. N. SUN[2]

Much work has been done within the last decade on the zonation structure of shoot apices, but recent investigations on root apical meristems are surprisingly few. Perhaps the earliest study of the root apex is that of Nägeli (1845). Later workers, such as Janczewski (1874), Eriksson (1878) and Flahaut (1878), classified root meristems according to their interpretation of the histogen theory. The present study deals only with the zonation of the apical meristem of soybean primary root. A brief outline of the literature on the structural differences among root apices of Leguminosae will be presented.

Janczewski (1874) described five types of promeristems for the phanerogams. In his fourth type, for which the roots of some Leguminosae (*Pisum sativum* and *Phaseolus vulgaris*) furnish examples, all tissues (the central cylinder, cortex, epidermis and root cap) originate from a common meristematic zone.

Eriksson (1878) distinguished four types of root apices for dicotyledons. His third type corresponds to Janczewski's fourth type, being characterized by the fact that all of the primary tissues of the root originate from a common meristematic zone. In this class he places the following species of Leguminosae: *Vicia sativa, V. narbonensis, Pisum sativum, Cicer arietinum, Phaseolus multiflorus, Lathyrus odoratus, L. latifolius, Robinia Pseudo-Acacia,* and *Cassia glauca.* Eriksson's fourth type, on the other hand, is characterized by the presence, at the apex of the root, of two different meristems, a plerome and a group of common initials. The former gives rise to the central cylinder. The latter gives rise to the cortex, epidermis and root cap. The root cap consists of two sharply defined parts: the columella and the peripheral portion. The columella is derived from the common initials by transverse cell divisions while the peripheral part of the root cap is derived from the common initials by tangential cell divisions. In this group he placed *Lupinus nanus, L. mutalilis, L. hybridus, L. albus, L. grandiflorus, L. dunetti, Mimosa pudica* and *Acacia lophanta.*

Flahaut (1878) examined individuals of three hundred and fifty species of phanerogams and found that those examined in the genera *Lupinus, Cercis, Gymnocladus, Guilandinia, Acacia* and *Mimosa* had distinct stelar

[1] This work was done at the Ohio State University, Columbus, Ohio. The author wishes to thank Dr. R. A. Popham for his kind advice during the investigation.

[2] Present address: St. Louis University, St. Louis, Missouri.

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initials and a common group of initials from which developed cortex, epidermis and root cap.

Tiegs (1912) reported three histogens, plerome, periblem, and protoderm-columella in the promeristem of roots of three species of Leguminosae (*Vicia villosa* lateral roots, *Pisum sativum* and *Trifolium repens*). The central cylinder originates from the plerome, the cortex from the periblem and the epidermis as well as the root cap from the protoderm-columella initials.

Neuman (1939) and V. Guttenberg (1947) found that in *Mimosa* and *Lupinus*, the promeristem consists of plerome, periblem, protoderm and columella initials. The plerome and periblem originate from a central cell. The central cylinder is derived from the plerome, the cortex from the periblem, the columella of the root cap originates from columella initials. The peripheral part of the root cap originates by periclinal divisions in the "dermatogen" according to Neuman.

Studies on *Arachis* (Yarbrough 1949), on *Pisum* embryo (Reeve 1948) and old primary root (Popham 1955) and on *Phaseolus* embryo (Sterling 1955) show the organization of the root apices as Janczewski's type IV. However, Popham (1955) pointed out that Janczewski's type IV is the one which exists in old primary and lateral root apices but not in the very young primordia of these roots.

The only investigation on zonation in the soybean (variety Mammoth yellow) root tip which has come to the authors' attention is that of Bell (1934). Bell found that the pattern of development corresponded to that of Janczewski's fourth class of angiosperms, namely, that the stele, cortex, epidermis and root cap, instead of arising from definite histogens, originate from a common group of meristematic cells. The results of the present study, however, indicate a more complex root apex organization in the soybean.

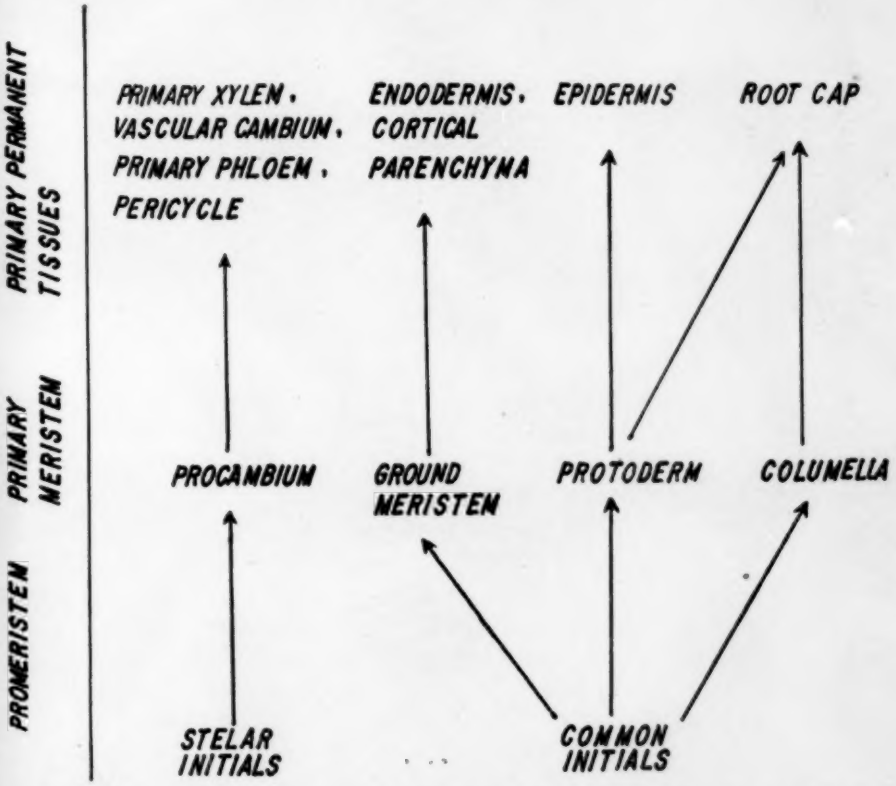
Materials and methods. The method of culturing the soybean plants (Monroe variety of *Glycine max* (L.) Merrill), and the technique used in the preparation of microscopic slides are essentially the same as described in an earlier paper (Sun 1955), except that only aerated primary roots were used for this investigation. The root tips were cut 6–7 μ thick.

General pattern of zonation. No distinct histogens can be recognized in the pro-meristem of primary roots of soybean which were collected from elder plants (fig. 4). However in the root promeristem of soybean embryos, mature seeds, and one or 3-day-old seedlings[3], the central procambial cylinder has a clear cut initial group (plerome); but the other primary meristematic tissues show no such precise site of origin (figs. 1, 2 & 3).

A group of initials which lie beneath the plerome undergo transverse

[3] This and similar expressions of time will refer to the number of days following the time when soybean seeds, which had been soaked for 24 hrs., were first put into germination crocks.

divisions, forming the columella of the root cap. The ground meristem[4] appears to lie peripherally to the common initials where the cortex, epidermis and the peripheral region of the root cap have a common origin. The development of the primary root of the soybean may be represented schematically as follows:



The stelar initials (plerome) and their derivatives. Two to six cells (as seen in median longitudinal sections) constituting the stelar initials (plerome) are situated at the apex of the central cylinder. They usually appear rectangular, pentagonal or hexogonal in both cross and longitudinal median sections. There are no intercellular spaces in the tissue. The isodiametric cells are thin-walled, non-vacuolated, and 6 to 12 μ in diameter.

The procambium, derived from the stelar initials, is composed of cells in vertical rows. This tissue consists of densely staining, slightly longitudinally elongated cells. In cross sections the cells appear rectangular, pentagonal or hexagonal. There are no intercellular spaces in the tissue.

[4] The ground meristem, protoderm and columella are derived from a group of initials, this group of initials will be referred to as *common initials*.

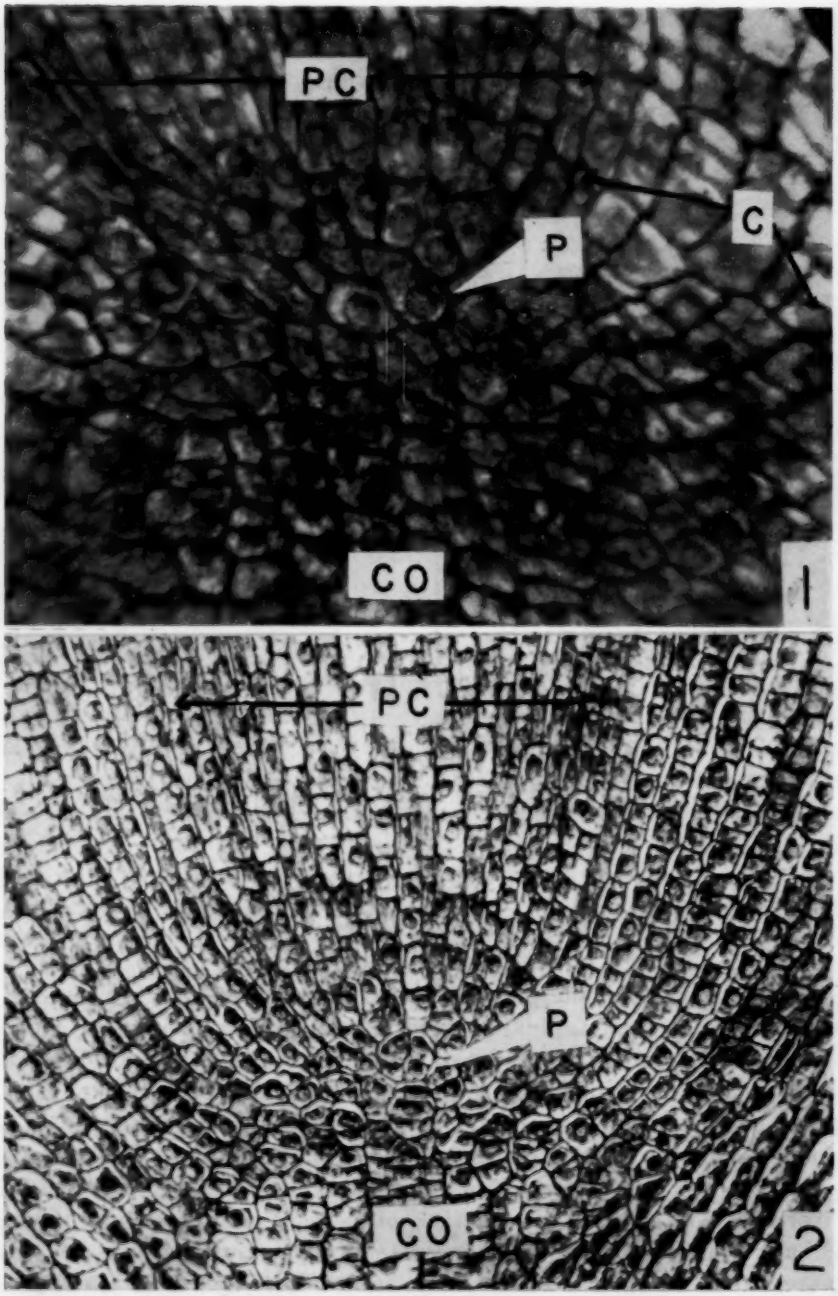
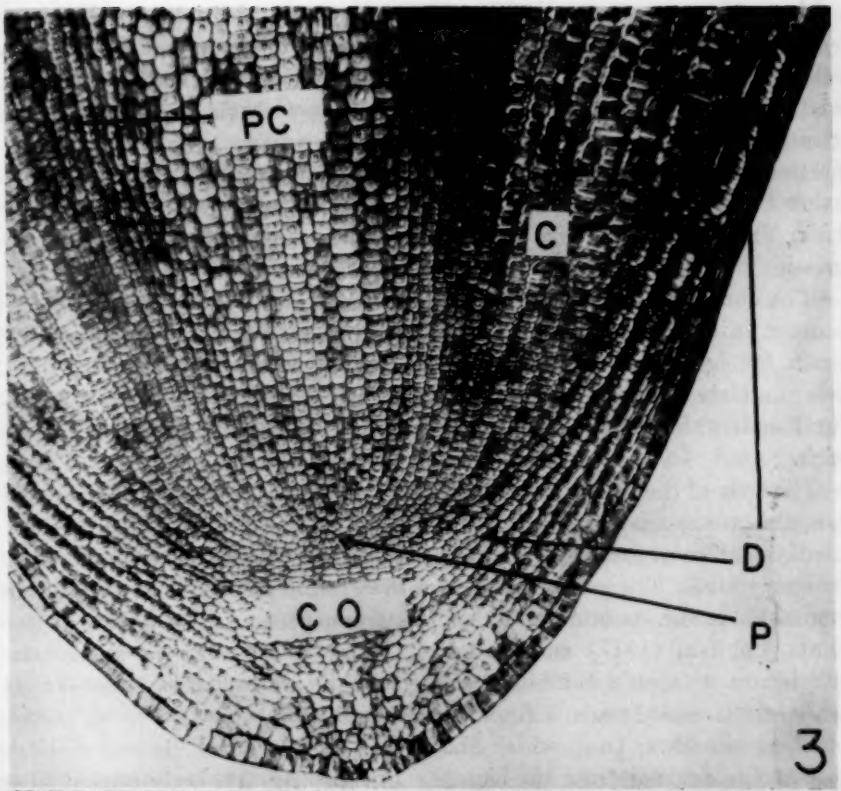


FIG. 1. Photomicrograph of a median longitudinal section of the root promeristem of an immature embryo illustrating the plerome and common initials. Magnification × 675. FIG. 2. Photomicrograph of a median longitudinal section of the root meristem of the primary root of a 3-day-old seedling illustrating the plerome and common initials. Magnification × 336.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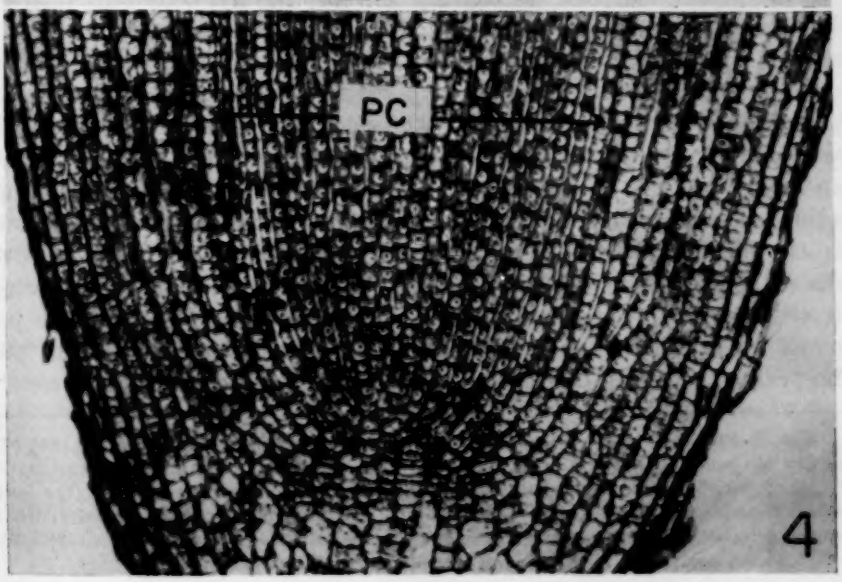
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At a distance of about 200 μ behind the stelar initials the cells of the central region of the root enlarge and develop conspicuous vacuoles. These cells are the forerunners of the central portion of the primary xylem. At this level, the group of cells which alternate with the projections of the tetrarch primary xylem differentiate into primary phloem. Portions of the pericycle adjacent to the primary xylem ridges are two to three cell layers thick while portions next to the phloem are one to two cell layers thick. The pericycle is composed of cells with dense cytoplasm and large nuclei.

The common initials and their derivatives. In longitudinal section, the common initials of the ground meristem, protoderm and columella appear as six to eight tiers of small non-vacuolated cells which lie beneath the stelar initials. In cross section, the cells appear pentagonal or hexagonal. Forty cells which were measured were 16 to 20 μ in diameter and 6 to 10 μ thick.

The cells of the ground meristem do not stain as deeply as the procambial cells and are much larger. Small intercellular spaces are characteristic of this tissue. The ground meristem is derived from the peripheral cells of the common initials. The mode of origin of the ground meristem is very different from that in the roots of many of the angiosperms. In certain species of plants, Popham (1947) and Williams (1947) found that the meristematic endodermis acts as a cambium giving rise to all cortical tissue. No such meristematic endodermis is found in the soybean root.

The protoderm, from which the epidermis is derived, is one cell layer wide and is derived from the common initials (fig. 3). Only anticlinal cell divisions occur in the epidermis which therefore remains a single layer of cells.

In the root cap, there are two sharply defined regions: the columella and the peripheral part of the root cap. The columella is derived from common initials by transverse cell divisions while the peripheral part of the root cap is derived from the protoderm. The columella consists of regular longitudinal rows of highly vacuolated cells in the central portion of the root cap. In the formation of the peripheral region of the root cap, only the cells of the protoderm divide periclinally. Each row of cells which is derived directly from the protoderm remains a single row of cells (fig. 3). This pattern of division is the same as that found in *Sinapsis alba* (Wagner 1939). The peripheral region of the root cap adjacent to the columella is nine to

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FIG. 3. Photomicrograph of a median longitudinal section of the primary root of a one day old seedling illustrating the plerome and common initials and the organization of tissues derived from it. Magnification × 145. FIG. 4. Photomicrograph of the longitudinal section of the primary root of a 8-day-old seedling illustrating the promeristem as a common transversal meristematic zone. Magnification × 245. Explanation of symbols: *c*, cortex; *co*, columella; *d*, protoderm; *p*, plerome; *pc*, procambium.

twelve cell layers thick. The number of rows gradually becomes smaller, until, at a distance of 3 mm. from the tip, it is one cell layer thick.

Comparison of apices of primary roots of various ages. The root apex of a mature seed is more massive than the primary root apex of a seedling (table 1). The root apex of a mature seed has a diameter of 625 μ (average of seven roots), whereas the apex of 14-day-old seedlings has a diameter of 344 μ (average of seven roots). The measurements, in both cases, were taken in a plane through the stelar initials.

Table 1 shows the number and thickness of cell layers in the various zones of the root apex of mature seeds and 3-day, 8-day, and 14-day seedling primary roots. The procambium is 28 cells in diameter (average of 5 roots) in the roots of mature seeds, as compared to 19 cells (average of 5 roots) in the primary root of 14-day seedlings. The ground meristem in the root of a mature seed is thicker than that of the primary root of seedlings, though the number of cell layers is approximately the same in both mature seed and seedling roots. The columella, on the other hand, is shorter and consists of fewer cell layers in the root apex of a mature seed than in seedling apices. The length of the columella and thickness of the peripheral part of the root cap increased gradually with the age of the root, while the thickness of the ground meristem and procambium decreased during the time interval covered in these experiments.

Discussion. Eriksson (1878) and Flahault (1878) stated that the root apices of some genera of Leguminosae consist of two histogens: the stelar initials (plerome) and the common initials of cortex, epidermis and root cap. The same marked zonation was found in the embryos and young seedlings of soybean root apices. However, the root apices which were collected from 5 day to 14 day old soybean plants show that all tissues originate from a common meristematic zone as Bell (1934) suggested. The different organization of root meristems in lateral root primordia and older lateral roots of *Pisum salvatum* has been reported by Popham (1955). Diversity of organizations in the root apical meristems of the same species was found by many workers. Foster (1942) pointed out that the present confusion as to the various types of root apices results from (1) the failure to trace the complete history of root apex from the embryo to the adult plant, and (2) the failure to recognize possible differences in details of cellular structure between the apex of the primary root and the apices of the lateral roots.

Eriksson (1878) found two sharply defined regions, the columella and the peripheral region, in the root cap of *Lupinus*. In the soybean the boundary between the columella and the peripheral portion of the root cap are fairly sharp and are obviously of different origin. In *Lupinus*, Eriksson found that the columella originates from the common initials by

TABLE 1. *Diameter of the primary root, and number and thickness of cell layers of different zones in primary roots of the mature seeds and seedlings of various ages cultured in aerated solution.*

	Mature seed		Seedlings					
			3-day-old		8-day-old		14-day-old	
	No. of cell layers	Thickness of cell layers in μ	No. of cell layers	Thickness of cell layers in μ	No. of cell layers	Thickness of cell layers in μ	No. of cell layers	Thickness of cell layers in μ
Procambium	24–30	240–425	20–28	255–320	18–20	170–212	18–22	127–161
Average[a]	28	406	26	296	19	203	19	156
Ground meristem	9–10	212–255	9–10	163–187	8–9	102–127	8–9	85–92
Average[a]	9	238	9	172	8	118	8	88
Columella	18–20	228–256	21–22	297–314	22–25	323–374	23–26	336–391
Average[a]	19	242	21	296	23	342	24	372
Diameter of the primary root		552–680 μ		484–612 μ		382–467 μ		323–382 μ
Average[b]		625 μ		550 μ		436 μ		344 μ

[a] The values in each case represent the range of 5 measurements. Measurements of procambium and ground meristem were taken at a level of 160μ behind the stelar initials. Measurements of the columella were taken from the end of the stelar initials to the root tip.

[b] These values represent the range of 7 measurements which were taken in a plane through the stelar initials.

transverse cell divisions while the peripheral part originates from the common initials by tangential cell divisions. In the soybean, similar transverse cell divisions were found in the columella whereas the peripheral portion of the root cap is derived by periclinal divisions of the protoderm.

Brumfield (1943), by mapping chromosomal rearrangements occurring during mitoses in *Vicia* root after treatment with X-rays, was able to show that the abnormalities occurred in cells of segments of the root extending from the center to the periphery. The shape of these segments suggested to Brumfield the possibility that the whole root was derived from three or four "apical cells". The present study has revealed no "apical" or "central" cells in the soybean root such as Brumfield (1943), Neuman (1939), and V. Guttenberg (1940, 1947) have suggested for other Leguminosae.

SUMMARY

1. The type commonly known as Janczewski's type IV is the one which exists in older primary root apices of soybean but not in the embryos and seedlings of these roots. The present study has revealed no "apical" or "central" cells in the soybean root.

2. The primary root tip of soybean consists of three regions: the promeristem, the primary meristems, and the primary permanent tissues.

3. In the root apices of embryos and seedlings, the promeristem consists of two histogens: the plerome and the common initials. The procambium is derived from the plerome (stelar initials) while the ground meristem, protoderm, and the columella of the root cap are derived from a group of common initials.

4. The root cap consists of two parts: the columella and the peripheral portion. The columella is directly derived from the common initials whereas the peripheral part of the root cap is derived from protoderm.

5. The procambium gives rise to the primary xylem, primary phloem, cambium, and pericycle. The ground meristem gives rise to the endodermis and cortical paranchyma. The epidermis is derived from protoderm.

6. The root apices of the mature seeds are more massive than those of seedling primary roots of various ages studied.

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SPONTANEOUS PRODUCTION OF A MORPHOLOGICALLY DISTINCT, FERTILE ALLOPOLYPLOID BY A STERILE DIPLOID OF ASPLENIUM EBENOIDES

W. H. WAGNER, JR. AND ROBERT S. WHITMIRE

Asplenium ebenoides was described as a new species of fern in 1865 by R. R. Scott. The following year, M. J. Berkeley declared "Scott's spleenwort" a natural hybrid between *A. platyneuron* and *A. rhizophyllum;* and for a number of years there was brisk argument over Berkeley's conclusion (Weatherby 1949). Although the alleged parents had but little superficial resemblance to one another, and did not suggest plants closely enough allied to interbreed, *A. ebenoides* did, nevertheless, seem intermediate between them. Moreover, practically all individuals of the presumed hybrid that were discovered during the early knowledge of this plant were single specimens, and quite clearly sterile. However, the later discovery of a population of wholly fertile plants of the intermediate at Havana Glen, Alabama, gave impetus to the arguments of those who considered it a normal species; and the question of its hybridity was not resolved until Slosson in 1902 produced the intermediate artificially in culture by growing together gametophytes of the presumed parents.

Recently it was determined that the ordinary sterile form of *Asplenium ebenoides* has $2n = 72$ chromosomes. At spore production there is lack of pairing of chromosomes in meiotic prophase, and 72 univalents are formed, suggesting that the chromosomes of the parents are so unlike genetically that the normal mechanism of reduction division is abortive. The plants are thus unable to reproduce by typical sexual reproduction. On the contrary, the fertile population of *A. ebenoides* which thrives in Hale County, Alabama, does undergo typical sexual reproduction, since the plants have double the chromosome number of the ordinary sterile diploid. The Alabama form is a tetraploid, with $2n = 144$, and with 72 normal bivalents at meiosis (Wagner 1954). Allopolyploids of the latter type are now known to be not at all unusual among ferns and other vascular plants.

The experiment to be reported here—in which a test of whether fertile, diploid spores could be produced by a sterile, diploid sporophyte was carried out—seems to be the first of its kind, and is sufficiently noteworthy to warrant the description that follows. The experiment resulted in a small number of new allopolyploid plants which turned out to be readily distinguishable morphologically from the Alabama wild type of allopolyploid.

The new allopolyploid was obtained under artificial conditions by sowing large quantities of spores and loose sporangia on sterile culture media.

The spore material was removed from leaves of sterile *A. ebenoides* in the University of Michigan Botanical Gardens collection found originally on shale bluffs by the old Chesapeake and Ohio Canal north of Martinsburg, Montgomery Co., Maryland. Conditions at the latter locality are optimal for interbreeding between *A. platyneuron* and *A. rhizophyllum,* the two parental species growing together, but scattered over the rather dry, mossy rocks. When the locality was first discovered (Wagner 1946), it was thought that the form of *A. ebenoides* found there might be fertile since there were several plants, but subsequent laboratory study showed that they were sterile diploids. During the decade 1946–1956, a number of visits to the Montgomery County locality always revealed a small number of hybrids, varying in age from tiny young sporophytes with leaves of the juvenile type, to fully grown, soriferous individuals. Although the new allopolyploid which was derived from the sterile progenitors differs considerably in its morphology from the Alabama wild type, it does resemble closely the sterile diploid plants from Maryland.

We are indebted to Mrs. Ann Barto Williams, who prepared the original cultures of spores and began the experiment upon which this report is based; to the Staff of the University of Michigan Botanical Gardens, for growing the later stages of the sporophytes; to Miss Clara S. Hires of the Mistaire Laboratories for supplying living material of the Alabama *Asplenium ebenoides;* and to Dr. G. Ledyard Stebbins of the University of California for his criticisms and suggestions.

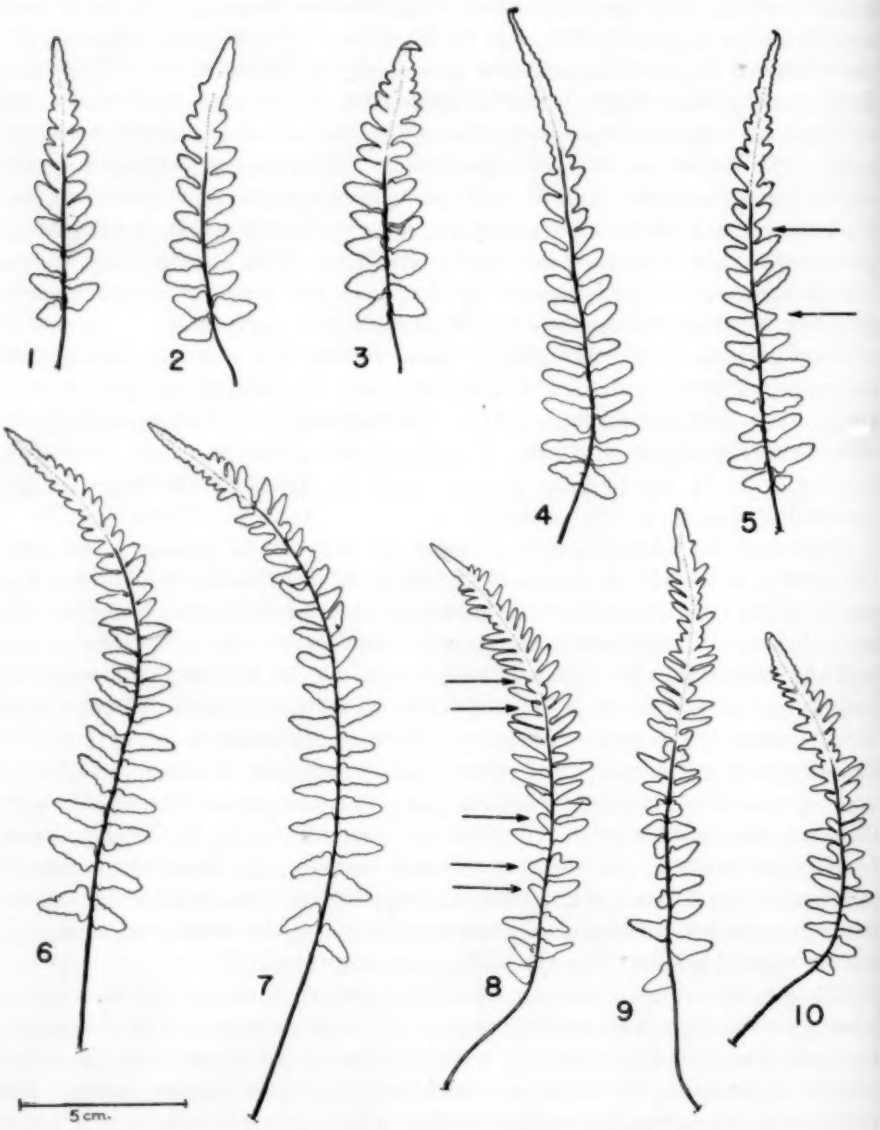
Production of the allopolyploid. Soriferous leaves of diploid plants of *Asplenium ebenoides* were washed violently under tap water to remove all foreign spores. The spores were then collected by drying the leaves in clean envelopes. Sterile agar solutions containing Beijerinck's and Knop's solutions were prepared in covered glass dishes, and the spore material was tapped on October 26, 1953, from the envelopes onto the surface of the nutrient agar. The earliest, microscopic germinating gametophytes appeared (or were first noticed) during January, 1954. These usually arose in clusters of three or four, growing through the walls of sporangia, or as individuals from free spores on the surface of the agar. The vast majority of the spores, within the sporangia and lying free upon the agar surface, were distorted and abortive, and did not germinate at all. There were approximately 25 gametophytes in total for all five culture dishes, although some of those in the tufted groups were dwarfed by overgrowth, and some may not have been visible at all. The number of gametophytes which developed, compared to the full number of sporangia and spores that were sown, was certainly very small. No practical way of estimating the number was devised at the time, but the total of the gametophytes could have represented no more than one gametophyte to several hundred spores, and probably much

less. Growth of those gametophytes which did form was rapid during February, March, and April, 1954, and by May 3rd, the first young sporophytes were noticed among the clustered gametophytes. These were well enough developed by May 31st to transfer to neutral soil in pots, and by the fall of the same year they were large enough to transfer individually to larger pots at the University of Michigan Botanical Gardens. A year later, many of the leaves bore sori, and at this time the sporangia were examined and found to contain normally developed spores; these spores were subsequently germinated and found to be wholly viable, as will be described below. Chromosome counts of squashes of this material revealed approximately $2n = 144$ in somatic tissue, and $n = 72$ in sporogenous tissue.

Comparison of the two allopolyploid forms. The culture allopolyploid contrasts with the Alabama wild type in an ensemble of characters, both sporophytic and gametophytic. Their contrasts include features of laminar color texture, outline of blade, breadth of lobes, regularity of lobulation, denticulation of the laminar margin, and the form of the edges of the prothallial wings.

The new allopolyploid is manifestly paler green in laminar color than the wild type in plants grown under identical greenhouse conditions. The colors of the two entities were estimated in indirect daylight using the color standards of Villalobos-Dominguez and Villalobos (1947): the *hue* of the leaf surface in both is "Lime (Verde Limón)." In *degree of chromaticity* both forms lie in the range 2° to 7°, but in *lightness value* different individual leaves of the culture allopolyploid fit in the range 6–9, and the wild allopolyploid in the range 5–7. The relative darkness of color in the wild type is especially evident if whole, living plants are placed side-by-side with those of the culture-produced type in clear daylight. In freshly dried herbarium material, the color differences remain approximately constant. Texturally, the lamina of the new allopolyploid is thinner than that of the wild type, the latter being somewhat more leathery, the former more papery, but no way of quantifying this difference was found.

The blade outline of the culture allopolyploid is broader than that of the wild type (Cf. figs. 1–6, and figs. 8–10). This was determined by measuring the total length of the blade and dividing this by the width of the broadest part of the blade as measured across the adjacent and opposite pinnae. For the former, blade-length/maximum blade-width averages 4.6, with a range of 3.6 to 6.5; for the latter, the value is 6.2, the range 5.0 to 7.3. The individual pinnae and lobes of the culture type are considerably broader on the average than those of the wild type, those of the former averaging 4.2 mm. in breadth as measured in the middle of the segments (the range to the nearest half-millimeter, 3.0–5.5); those of the wild type, 3.3 mm. (3.0–4.0).



FIGS. 1–6. Leaves from culture allopolyploid. FIGS. 1, 2. Plant #4. FIG. 3. Plant #3. FIGS. 4, 5. Plant #1. FIG. 6. Plant #2. FIG. 7. Leaf from original sterile plant from Montgomery Co., Maryland, grown under greenhouse conditions. FIGS. 8–10. Leaves from wild type of allopolyploid, Hale Co., Alabama, grown in greenhouse. (The arrows point to dwarfed, irregular lobes.)

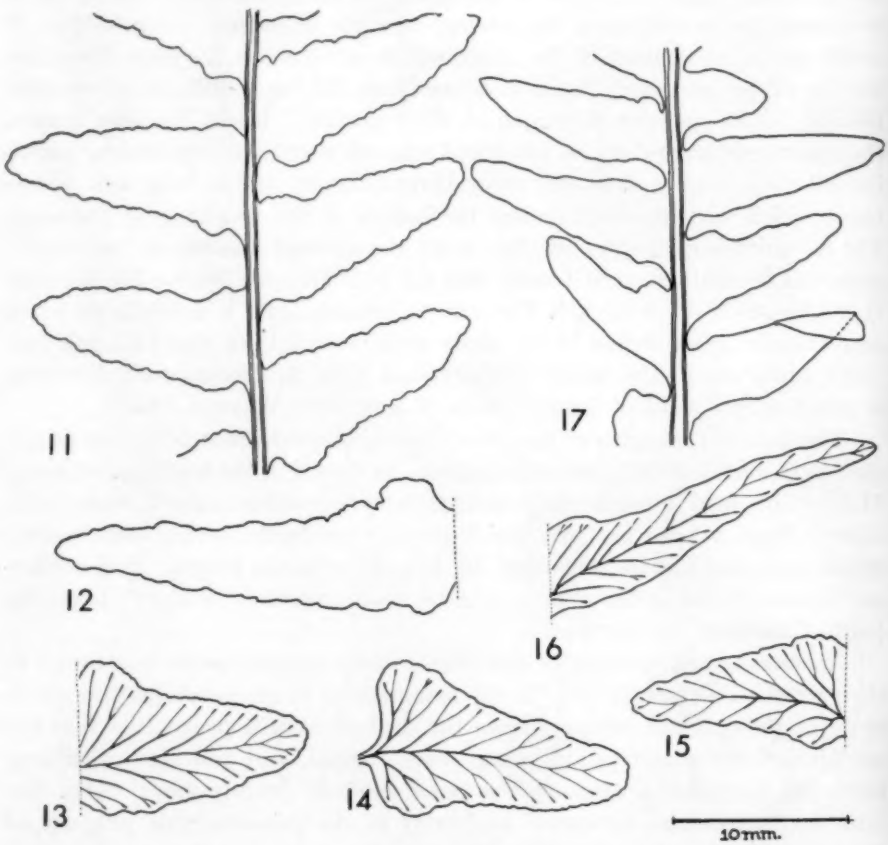
One of the most interesting differences between the two forms involves the relative numbers of "abortive" segments, i.e., those segments which are

only one-half or less the length of those above and below them (examples indicated by the arrows in figures 5 and 8). These dwarfed segments are generally not only shorter but also of different shape, being rounded as a rule at the apex, although occasionally some of them are like miniature normal segments. This phenomenon of irregularity in the lobulation of the blade is expressed much less strongly in the culture allopolyploid than in the Alabama type, the leaves of the latter, in fact, commonly appearing to be monstrous or deformed on account of their numerous irregularities. It is the apical one-fourth of the blade which tends to be the most irregular, but for simple and easily-made measurements, the tip is difficult to interpret because of the relative shortness of the "normal" lobes. For this reason, the number of irregularities per frond was arbitrarily determined by counting all those segments in the lower three-quarters of the long axis of the blade which were one-half or less the length of the neighboring segments. For the culture allopolyploid (figs. 1–6), the average number of "abortive" segments in medium-sized fronds was 0.5 (0.0–3.0) per blade; for the wild type (figs. 8–10), 6.3 (3–12). The culture allopolyploid is accordingly much more nearly symmetrical in its blade architecture than the Alabama one. (The *backcross* of the latter allopolyploid with *A. platyneuron*, however, is practically devoid of irregularities of any sort; Wagner 1956).

The segment margins of the laboratory-produced plant are more or less shallowly, but definitely, angular-dentate, as shown in the tracings in figures 11–14. The wild allopolyploid is extremely smooth-margined, essentially entire; those pinnae or lobes which are not perfectly entire show merely gentle marginal undulations (figs. 16, 17). Even in the largest, most soriferous leaves of the latter that would be most expected to show them, the toothed margins are not found.

An unexpected contrast of the plants under consideration was found in their prothallia (figs. 21–24). It was first noticed in the gametophytes which arose in the original cultures from the diploid hybrid progenitor that the margins of the gametophytic wings were ragged, and provided with long tooth-like marginal projections composed of 5–12 (rarely more) cells. The same structures also appeared uniformly in the gametophytic progeny of the second generation (fig. 21). The peculiar processes thus appeared at the time of origin of the allopolyploids. For growing the gametophytes of the culture allopolyploid (as well as comparative material of the other entities involved) Knop's nutrient solution was chosen: Standard petri plates were used as culture containers, and the spores were removed from the sporangia and distributed over the surface of the culture medium. Two plates each of culture allopolyploids #1, #2, and #3, were then placed under controlled light conditions with continuous light and at a temperature of 20°C, the same conditions under which gametophytes of the wild type

of allopolyploid and the two parental species were grown. First evidence of germination was observed after a period of 8 days, and the germination appeared to be entirely normal. Antheridia and archegonia were observed on the prothallia after a period of 28 days. The germination period and time required for the development of mature gametophytes compares closely with other members of the genus.

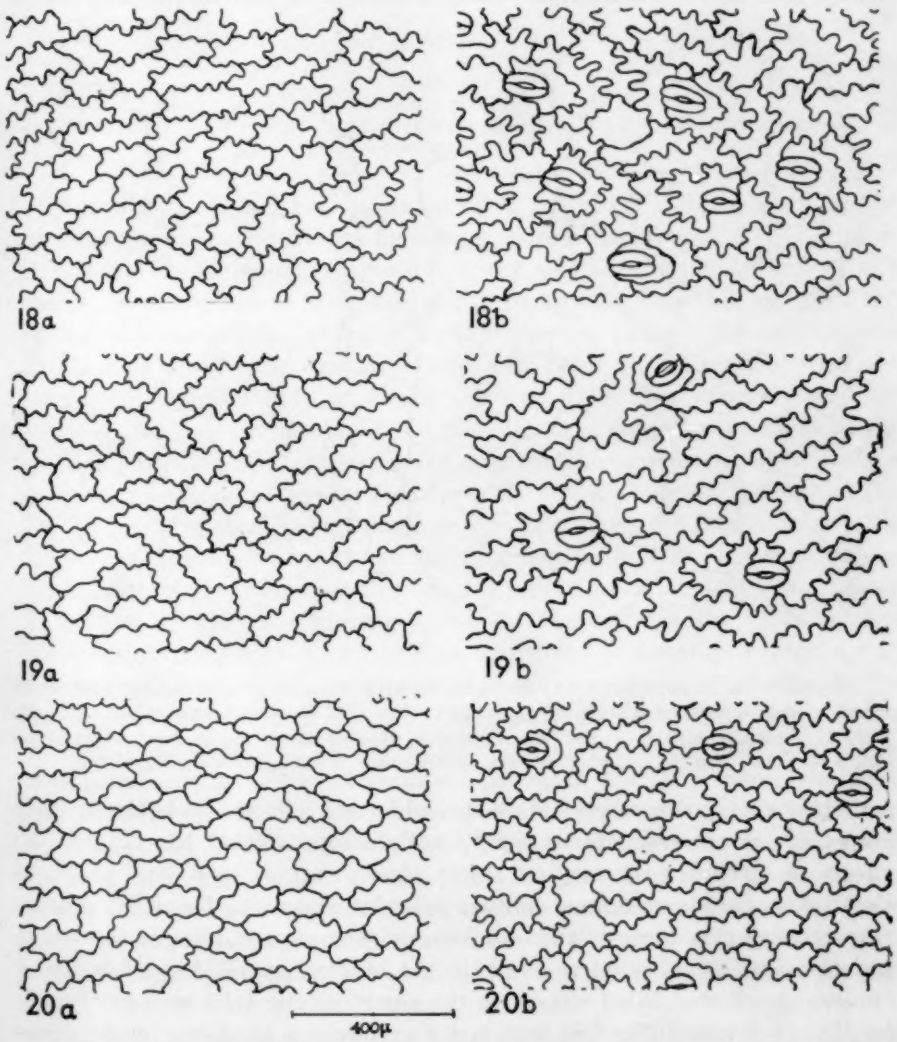


FIGS. 11–14. Median leaf segments of culture allopolyploid. FIG. 11, Plant #2. FIG. 12, Plant #1. FIGS. 13, 14. Plant #4. FIG. 15. Leaf segment of original sterile diploid from Montgomery Co., Maryland. FIGS. 16, 17. Leaf segments of wild type of allopolyploid, Hale Co., Alabama.

The projections of the mature gametophytic margins of the culture allopolyploid are provided at their apices with single-celled "papillae," rounded-oblong in outline (fig. 21b). The large marginal projections create a "ragged" appearance which is wholly lacking, not only in the prothallia of the wild form of allopolyploid (fig. 22), but absent also in the prothallia

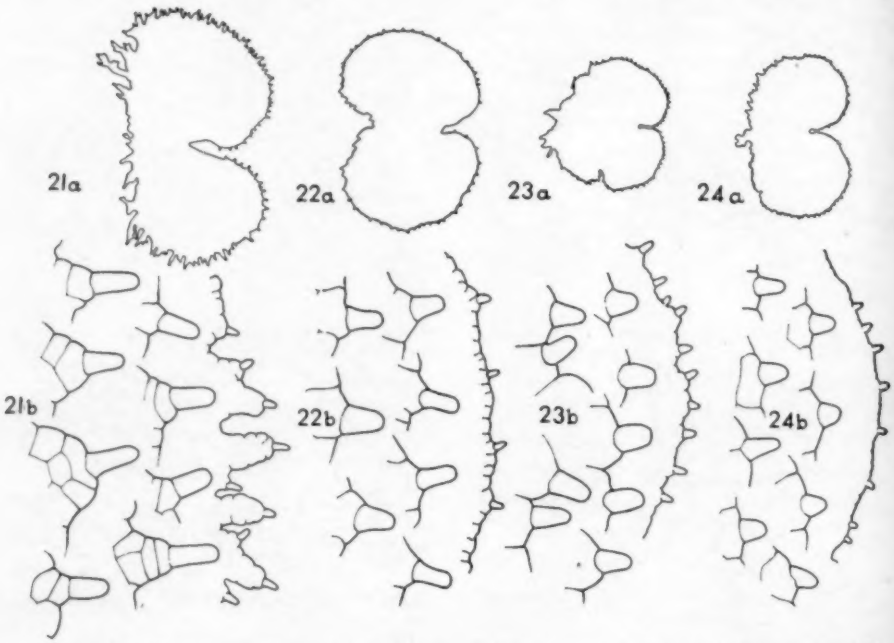
of both *Asplenium platyneuron* (fig. 23) and *A. rhizophyllum* (fig. 24), the original parents, growing under the same conditions. All three of the latter entities produce the single-celled marginal papillae, but these are borne on an otherwise essentially smooth prothallial margin, as shown in figures 22b, 23b, and 24b.

As was found to be true previously in comparing forms of different polyploid levels in this group (Wagner 1954), the new allopolyploid spleen-



FIGS. 18–20. Epidermal cells: a, upper epidermis; b, lower epidermis. FIG. 18. Wild allopolyploid, Hale Co., Alabama. FIG. 19. Culture allopolyploid. FIG. 20. Original sterile diploid from Montgomery Co., Maryland.

wort possesses cells of larger size on both epidermal surfaces (figs. 18–20). Both the guard-cells and the contiguous epidermal cells appear to be affected by the increase in chromosome number, and the culture allopolyploid has cells of approximately the same size as those of the wild type. Since all of these plants were grown under approximately the same conditions at the University of Michigan Botanical Gardens, their epidermises are probably comparable, but one may question whether all specimens grown under varied and extreme conditions out-of-doors (or in the laboratory) would



FIGS. 21–24. Gametophytes (a) and gametophytic margins (b), including both whole margins and details of marginal "papillae". FIG. 21. Culture allopolyploid. FIG. 22. Wild type of allopolyploid. FIG. 23. *Asplenium rhizophyllum*, spores from Washington Co., Arkansas. FIG. 24. *A. platyneuron*, spores from Washington Co., Maryland.

be dependable in this respect, since the epidermal cells are probably strongly responsive to external growth conditions. Allsopp (1954) has studied the effects on *Marsilea* of varying sugar concentrations, and has produced striking changes in epidermal cell size in media containing 5 and 1% glucose respectively; this suggests that similar environmental studies of terrestrial plants might be initiated to evaluate the cytotaxonomic dependability of epidermal cell size. With respect to the gametophytic trichomes or "papillae," the cell-size differences were not very obvious, as shown in the drawings in figures 21b, 22b, and 23b. The allopolyploids seem only to average slightly longer as regards these structures.

The major differences of the culture allopolyploid and the wild type are summarized in Table 1.

TABLE 1.

	Culture Allopolyploid	Alabama Allopolyploid
Color (Lightness value).	6–9	5–7
Texture.	Chartaceous.	Leathery.
Blade: Length/Breadth.	4.6 (3.6–6.5)	6.2 (5.0–7.3)
Median segments: breadth (mm).	4.2 (3.0–5.5)	3.3 (3.0–4.0)
Number of "abortive" segments.	0.5 (0–3)	6.3 (3–12)
Segment margins.	Shallowly toothed.	Entire.
Gametophyte.	Multicellular marginal projections.	Smooth-margined.

Discussion. If as many as twenty-five polyploid gametophytes can be produced in five culture dishes by sowing spore material from sterile, diploid *Asplenium ebenoides*, one may inquire why new allopolyploid forms of this species have not arisen more frequently in nature. Probably not one, but rather an inter-related series of factors operate against the spontaneous appearance of allopolyploid populations of ferns in nature, reducing the chances of establishment statistically far below those from spores of already-established or normal species. (1) Evidently only a small percentage of the total of spore tetrads form with the doubled chromosome number. Only a fraction, therefore, of the spores of sterile, diploid hybrids are viable. (2) Such "good" spores as are formed and released from sporangia must settle in an appropriate microhabitat for germination and development. These microhabitats are rarely directly below a parent plant, and the spores must be carried by wind for varying distances. The appropriate conditions are narrowly restricted, even in localities where the parental sporophytes may be common or abundant, to soil surfaces and crevices in which exactly the right surroundings prevail. (3) Once having reached the appropriate ecological situation, the allopolyploid gametophyte is required to compete with gametophytes of the parental species which are vastly more abundant, and perhaps considerably better adapted for growth under these habitat conditions. (4) Even when the allopolyploid gametophyte succeeds in growing in a particular habitat, the tendency for growth to be divided into two phases—the juvenile or antheridial, and the mature or archegonial—may require cross-fertilization with another gametophyte for successful production of a new sporophyte. The chances for another polyploid hybrid gametophyte being close at hand seem very small. Indeed, the opportunities would seem greater for backcross hybridization, the allopolyploid with one or the other of the parents.

In the study of the Appalachian Aspleniums, the present experiment is

especially interesting because it represents the first time we have been able directly to compare the diploid sterile progenitor with its allopolyploid derivative. Furthermore, we have been able to compare a *de novo* allopolyploid with a well-known wild type of presumably the same genetic constitution of parental species. Between the original diploid and sterile progenitor, and its tetraploid and fertile derivative, there is no noticeable change in morphology, with the exception of some increase in epidermal cell size. In terms of laminar color, texture, blade outline, segment breadth, number of "abortive" segments, and the marginal denticulation, the $2n$ and $4n$ are a close match (as shown in figures 6 vs. 7; and 14 vs. 15).

On the contrary, the culture allopolyploid contrasts obviously with the well-known wild type from Hale Co., Alabama, in seven more or less striking respects. What the origin of these differences might be poses an interesting question. It is possible, of course, that the Alabama allopolyploid might have originated in ancient times and thus may have been able to evolve independently through mutation and selection to its present distinctive form, but its extremely narrow range in nature does not foster this hypothesis. On the other hand, the distinguishing features of these two allopolyploids might also have sprung into being suddenly if the genotypes of the original parents were different for each allopolyploid. Even seemingly trivial genetic differences where the parents are as distantly related as *Asplenium platyneuron* and *A. rhizophyllum* might be magnified in new combinations between them, and produce unexpectedly strong differences in the allopolyploids formed from different parental varieties in different localities.

Notwithstanding the low statistical probability of opportunities for formation of new allopolyploid populations, the great ranges and numbers of the parental species suggest that additional fertile populations of *Asplenium ebenoides* are still to be found in the wild. It may be suggested, too, from the present experiment, that if other allopolyploid populations are found in the future, they may well be morphologically different from the single natural population already known. As proposed above, the differences between such polyploids may stem not primarily from evolutionary factors such as mutation and selection acting on the allopolyploids, but instead mainly from more or less different genetical constitutions of the original parents. It would seem desirable to pursue this conclusion in the future with controlled experiments in which different allopolyploids would be artificially synthesized from different stocks of the parental species. The well-known variations observed between populations of other apparently allopolyploid North American ferns like *Dryopteris clintoniana, Asplenium pinnatifidum,* and *A. bradleyi* may have also arisen at least in part at the moment of their origin, from genetic differences already inherent in the parental germplasms, and they too would be subject to experimental study.

SUMMARY

1. The hybrid fern, *Asplenium ebenoides* (*A. platyneuron* × *A. rhizophyllum*) occurs in nature as a sterile diploid over a wide range, and also as a fertile allopolyploid limited narrowly to Hale Co., Alabama. *Asplenium ebenoides* has been synthesized in culture, and has been backcrossed with *A. platyneuron*, but no new fertile allopolyploids have been heretofore produced under experimental conditions.

2. A new and distinctive allopolyploid form of *A. ebenoides* arose spontaneously in cultures produced by sowing large numbers of spores and sporangia from a sterile diploid form collected in Montgomery Co., Maryland. A total of about twenty-five gametophytes, appearing as clustered groups or as solitary individuals, was produced among thousands of spores. Fertilization among these gametophytes yielded a uniform type of sporophyte, resembling the sterile diploid progenitor.

3. The new allopolyploid differs from the wild Alabama type in a number of characters, including the blade texture, blade color, outline of leaf, breadth of leaf-segments, number of dwarfed segments, form of the segment margins, and the outline of the gametophytic wings. The new allopolyploid reproduces as readily from spores as does the wild type.

4. The rarity of allopolyploid populations of ferns in nature is briefly discussed, and a series of factors is suggested to account for it: (1) the small number of polyploid spores produced by the sterile diploid; (2) the necessity for the polyploid spores to fall in narrowly defined microhabitats; (3) competition with the gametophytes of normal species in the same habitat; and (4) a tendency for gametophytes to require cross-fertilization.

5. Because of the close resemblance of the allopolyploid to its sterile diploid progenitor and because of its morphological distinctness from the previously known allopolyploid from Alabama, the suggestion is made that varying forms of species of this evolutionary origin may be due to genetic differences between parental races in different localities.

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FLAGELLARIA GUINEENSIS SCHUM.

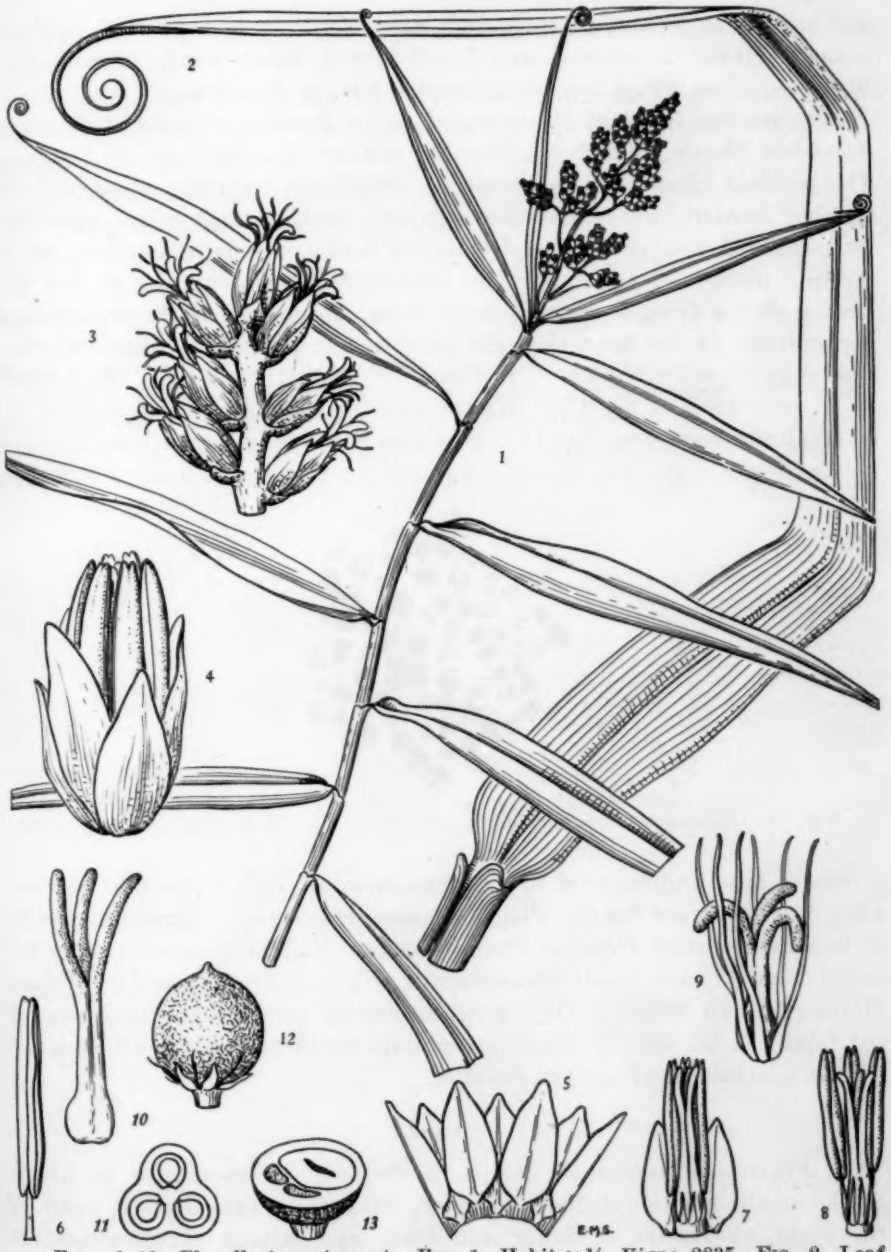
J. T. BALDWIN, JR. AND BERNICE M. SPEESE

Flagellaria L. is perhaps the best-known genus of the Flagellariaceae, a family of three genera and about ten species (Willis 1948) in the tropics and subtropics of the Old World and, according to Hutchinson (1946), derived from the Commelinaceae. *Flagellaria* consists of four or more species. *F. guineensis* Schum. is the only African representative of the family.

Herbarium material examined at Kew in 1949 indicates that *F. guineensis* has a geographic range from the Ivory Coast through West Africa to the Belgian Congo, across to Kenya, through East Africa to the Union of South Africa. On August 12, 1947, the senior author collected this species, at the end of its fruiting season, on sandy soil beside the Cess River near Bahtown in the Tchien District of Liberia: *Baldwin* 9015, U. S. National Herbarium, Smithsonian Institution. [See Baldwin (1950) for political divisions of Liberia.] This is the northernmost station known for *F. guineensis* in the western part of its range and the only Liberian record for the species.

Extensive travel (1947–1950) in West Africa and for a short time in the Belgian Congo resulted in only one other collection of *F. guineensis:* at Assuantsi, Gold Coast, January 15, 1950, where the plant was common at the edge of secondary forest and climbing to a height of thirty feet, with terminal panicles of white flowers (not yellow, as recorded by Hutchinson and Dalziel 1936) and with bright red, showy fruit: *Baldwin* 14029 (US). Similar notes on *R. M. Graham* 1531 (K), from Mida, Kenya, read: "Climbing or trailing plant on edge of forest or in bush. Flowers white. Fruits red in dense clusters. Twigs used by the Wasanya (a bush tribe) as a medicine for venereal disease." Though to judge by the number of specimens at Kew the species is fairly frequent in West Africa—especially in the Gold Coast, Dalziel (1948) reports no native uses for the plant.

The habit of *F. guineensis* and flower and fruit characters are shown in figures 1–13, which are reproduced from drawings made for us at Kew by Miss E. M. Stones under the supervision of Mr. E. Milne-Redhead. We are grateful to these individuals for their kind assistance. The figures are from the following specimens at Kew: *Vigne* 2835, from Axim, Gold Coast, with young flowers; *Vigne* 1441, from Aiviabo, Gold Coast, with mature flowers; *Chipp* 393, from Aseim, Gold Coast, with fruits. The plant is climbing. Leaves are sheathed and tendril-tipped. Flowers are perfect and borne in panicles. Perianth is 6-parted, 2-whorled, subpetaloid, hypogynous,



FIGS. 1–13. *Flagellaria guineensis*. FIG. 1. Habit, ×½ *Vigne* 2835. FIG. 2. Leaf, ×2¼ *Vigne* 2835. FIG. 3. Inflorescence, ×3 *Vigne* 1441. FIG. 4. Flower, ×9 *Vigne* 2835. FIG. 5. Perianth, ×6 *Vigne* 1441. FIG. 6. Stamen, ×9 *Vigne* 2835. FIG. 7. Dissected Flower, ×6 *Vigne* 2835. FIG. 8. Stamens and Pistil, ×6 *Vigne* 2835. FIG. 9. Filaments and Pistil, ×6 *Vigne* 1441. FIG. 10. Pistil, ×9 *Vigne* 2835. FIG. 11. Ovary Diagram. FIG. 12. Fruit, ×3 *Chipp* 393. FIG. 13. Fruit Section, ×3 *Chipp* 393.

and persistent. Stamens are 6, with free filaments and 2-celled, introrse anthers. Ovary is superior and 3-celled, with single ovule in each cell. Style is 3-lobed. Fruit is a berry about 6 mm. in diameter.

The mature fruits of *F. guineensis* are suggestive of those of *Nandina domestica* Thunb., though considerably smaller than the fruit of *Nandina*. The pendant clusters of red fruit of *Flagellaria* are truly handsome. In shrubby borders, where the vine supports itself among other vegetation by means of slender and tendril-tipped leaves, the fruit clusters afford striking patches of color. For this reason, seed were introduced into the United States from Assuantsi, Gold Coast, via the U. S. Department of Agriculture, in the hope that the plant might become an effective ornamental in the warmer parts of the country: Plant Introduction No. 184900.

F. guineensis at the Cess River station in Liberia has a $2n$-number of 36 small chromosomes (fig. 14). Root-tips and young leaves were fixed in

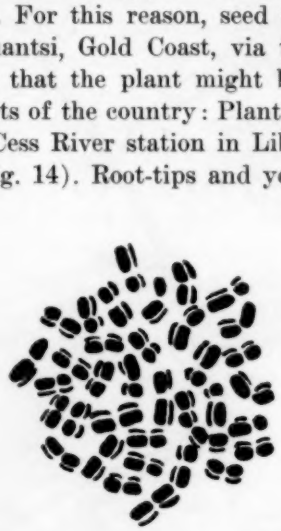


FIG. 14. Chromosomes of *Flagellaria guineensis*: $2n = 36$ in root-tip smear. × 3500.

Carnoy's fluid and smeared in propiono-carmine. This is the first chromosome-number report for the Flagellariaceae. Hutchinson claims this family to be a development from the Commelinaceae. Many representatives of the latter family have small chromosomes, while others have large ones; Darlington and Wylie (1955) recognize among various basic numbers for the family 6, 12, and 18. Chromosome data could be used as evidence for a close relationship of the two families.

SUMMARY

1. *Flagellaria guineensis* Schum. is the only representative in Africa of the small, monocotyledonous family, Flagellariaceae. Growth habit of the plant, characters of flower and fruit, and mitotic chromosomes are illustrated. The species has a $2n$-number of 36 small chromosomes and is the only member of the family that has been cytologically investigated.

2. A collection of *F. guineensis* by Baldwin in 1947 on the Cess River

extended the range of the species northward from the Ivory Coast into Liberia.

3. The clusters of red fruit of *Flagellaria* are strikingly handsome: seed were sent from the Gold Coast in an attempt to introduce this plant into American horticulture.

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A CYTO-TAXONOMIC STUDY OF SETARIA MACROSTACHYA (GRAMINEAE) AND ITS RELATIVES IN THE SOUTHWESTERN UNITED STATES AND MEXICO[1]

WILLIAM H. P. EMERY[2]

The genus *Setaria* contains several important species with wide distribution throughout the temperate and sub-tropical regions of the earth. It is perhaps best known through the agriculturally important *Setaria italica* (L.) Beauv., or foxtail millet, which is believed to have been cultivated since prehistoric times. Several additional species are economically important for certain regions, however, because of the forage and range cover they provide.

A group of closely related, perennial species of the genus *Setaria* from southwestern United States and Mexico have been examined in order to establish a taxonomic treatment which takes into account morphologically distinct populations. The following species are recognized in this study: *S. macrostachya* H. B. K. (*sensu stricta*), *S. leucopila* (Scribn. & Merr.) K. Schum., *S. texana* sp. nov., *S. villosissima* (Scribn. & Merr.) K. Schum., and *S. scheelei* (Steud.) Hitchc.

Preliminary investigation showed that each of these species is polyploid and that apomictic reproduction occurs in certain forms. The five species involved in the present study are assumed to be only a portion of a large agamic complex, the extent of which cannot yet be fully comprehended. To provide a collective reference to these five species, they are designated as the *Setaria macrostachya* complex.

The earliest taxonomic treatment involving a species of this complex was that of Humboldt, Bonpland, and Kunth (1815) who described a collection from the highlands of central Mexico as *S. macrostachya*. Since that time a number of other papers involving the taxonomy of this group have appeared. Probably one of the more important of these was Scribner and Merrill's monograph, "The North American Species of *Chaetochloa*" (*Setaria* is a *nomen conservandum*). In their treatment, the *S. macrostachya* complex is separated into seven distinct species. Hitchcock (1920, 1931, 1950) took a more conservative view and retained *S. scheelei* and *S. villosissima* as separate species but broadened the concept of *S. macrostachya*

[1] This study is a portion of a Ph.D. thesis submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy, University of Texas.

[2] The author wishes to express his appreciation to Dr. W. V. Brown and Dr. B. L. Turner of the Botany Department, University of Texas, under whose direction this investigation was carried out, and to Dr. Lloyd Shinners for the Latin diagnosis.

to include all the remaining populations of the *S. macrostachya* complex in one large polymorphic species. Hitchcock (1920) noted the possible existence of two morphologically distinct forms in *S. macrostachya*, but because of a number of more or less intermediate specimens he felt it impractical to draw specific lines between them. The growing economic and scientific interest in these rangeland grasses, however, has indicated a need for a reevaluation of the taxonomic status of several morphological forms included in *S. macrostachya* (*sensu* Hitchcock).

The present treatment is based on new information in the form of chromosome numbers, populational studies, and a reevaluation of morphological characters. Although this investigation does not provide the comprehensive data required for a complete analysis of an agamic complex (Babcock and Stebbins 1938), it does provide sufficient information of this restricted group to justify a new taxonomic evaluation. The information presented in this study allows the taxonomic entities of this complex to be distinguished with better clarity and in a more natural fashion than was previously possible.

Taxonomy. Species included in the *S. macrostachya* complex exhibit a wide phenotypic variability and it is frequently necessary to utilize a combination of characters to classify certain specimens. In order to facilitate identification of plants of the species recognized in the present study, the following artificial key is presented.

ARTIFICAL KEY TO *SETARIA MACROSTACHYA* AND RELATED SPECIES IN THE SOUTHWESTERN UNITED STATES AND MEXICO

1. Spikelets 2.9 mm. or more in length ..... *S. villosissima*
1. Spikelets less than 2.9 mm. in length
   2. Panicles 3–6(8) cm. long; culms branched above; spikelets 1.9–2.1 mm. in length ..... *S. texana*
   2. Panicles 6–25 cm. long (occasionally less on depaupreate specimens); culms rarely branched above; spikelets 2.0–2.5 mm. long.
      3. Fertile lemma of mature spikelet gibbous (inflated at base); fertile palea broad, slightly to strongly convex; sterile palea nearly as long as fertile palea ..... *S. macrostachya*
      3. Fertile lemma of mature spikelet not conspicuously gibbous; fertile palea flat or concave; sterile palea usually less than ¾ the length of fertile palea.
         4. Blades 4–9 mm. wide, flat or folded, rarely pubescent; panicle usually columnar; bristles usually appressed, 5–12(16) mm. long; culms mostly erect, caespitose, occasionally geniculate in robust specimens ..... *S. leucopila*
         4. Blades 9–15 mm. wide, flat, commonly pubescent; panicles usually tapering; bristles spreading, 10–35 mm. long; culms usually geniculate ..... *S. scheelei*

SETARIA VILLOSISSIMA (Scribn. & Merr.) K. Schum., Just's Bot. Jahresber. 28: 417. 1902. *Chaetochloa villosissima* Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 34. 1900. Holotype examined, (US) TEXAS: Duval Co.: San Diego, May 1897. *J. G. Smith.*

Description: The description of *S. villosissima* is the same as that given by Scribner and Merrill (1900).

Distribution: It is a rare species known only from a few widely scattered areas of Texas, from two collections in Arizona, and from a single collection in north-eastern Sonora, Mexico (Map 1).

Discussion: In view of the scattered distribution and apparent rarity of this species a population at Bear Mountain in Gillespie Co., Texas was studied in detail in order to provide a better basis for evaluating whether or not it should be considered as a natural group.

At this locality there is a granitic outcrop which is surrounded on all sides by limestone formations. The demarcation between limestone and granite is sharp and in most positions around the mountain the aspect of the vegetation changes markedly within distances of 100 ft. or less. Careful search of the limestone area failed to reveal a single plant of *S. villosissima.* Within less than 100 ft. however, the species could be observed to be the dominant grass on all slopes of the granitic outcrop.

A mass collection of the grass (*Emery 434–467*), including a selection of various growth forms was made. Subsequent examination of these specimens showed that in spite of some variation in over-all stature, there was little or no variation in the diagnostic characters of spikelets size or foliage pubescence.

Label information from herbarium specimens collected elsewhere indicates that *S. villosissima* has been found only on soils derived from igneous rock, agreeing with the writer's own field observations. The holotype of this species, reported to have been collected in an area where such soils are not known to occur, constitutes the only exception encountered. Numerous collections from the type locality (San Diego, Tex.) and from surrounding Duval Co. have been made during the past fifty years but not one additional specimen of *S. villosissima* has been reported.

In view of these facts, it is possible that an error may have occurred in the citation of San Diego as the type locality. Further credence is given to this possibility by the fact that in the U. S. National Herbarium there exists a second specimen of Smith's bearing exactly the same data as the holotype (*J. G. Smith,* San Diego, Texas. May 1897). This second specimen is *S. scheelei.*

Cytological information is available for only two collections of *S. villosissima* and therefore any extrapolation of the data for the species as a whole must be made with considerable reservation. The somatic chromosome number of these two plants is $2n = 54$. Microsporogenesis is completely regular with the formation of a high percentage of good pollen. Megasporogenesis is completely regular up to the formation of tetrads but development of the reduced gametophytic tissue appears retarded and apospor-

ous embryo sac initials develop from cells of the nucellus. A large portion of the progeny are assumed to result from apomictic reproduction.

S. *villosissima,* as circumscribed, presents no particular problem in terms of the systematics of the *S. macrostachya* complex and though apomixis has been demonstrated in two plants of this taxon, the present information does not appear to warrant a change in the treatment of *S. villosissima* at this time.

Representative specimens: MEXICO: COAHUILA: Canon de Milagro, *Stewart 1707* (GH, US); Near Tanque Vaionetta, *Johnston 8433* (GH). SONORA: Canon de la Bellota, *Santos 2098* (GH, SMU, US). UNITED STATES: ARIZONA: Without data, *Emersley 19* & *21* (US). TEXAS: Burnet Co.: Granite Mt., *Reed* (US). Gillespie Co.: Balanced Rock, *Silveus 7337* (US); *Cory 24523* (US): *Emery 434–467* (TEX). Jeff Davis Co: Musquiz Swamp, *Warnock T223* (US); Davis Mts., *Warnock 8037* (SMU). Presidio Co.: *Hinckley 2023* (US).

Setaria texana sp. nov.

Type locality: TEXAS: Kleberg Co.: 8 mi. west of Kingsville, Nov. 11, 1955. *Emery 515.* Holotype deposited at The University of Texas; isotypes to be distributed.

Description: Perennis 30–90 cm. altus, culmis erectis vel geniculatis compressis superne ramosis infra paniculam et plerumque infra nodes glabros scabris. Foliorum vaginae compresso-carinatae glabrae vel in carina scaberulae, margine superne ciliatae; ligula dense ciliata usque ad 1 mm. longa; laminae planae supra scabrae infra laeves vel scabrellae 5–20 cm. longae 2–5 mm. latae. Panicula spiciformis 2–8 cm. longa superne paulum angustata infra interdum interrupta vel lobata cum axi angulato scabro puberulo, ramuli minus quam 3 mm. longi; setae plerumque solitariae 3–10 mm. longae molles antrorse scabrae. Spiculae 1.9–2.1 mm. longae; gluma inferior trinervata spiculam ½ aequans, gluma superior quinquenervata spiculam ¾ aequans; lemma sterile quinquenervatum, lemma fertile tenuiter transverse rugulosum aequans; palea sterilis minuta vel paleum anguste ovatam fertilem usque ½ aequans. Chromosomata somatica 36.

Perennial 30–70(90) cm. tall. Stems wiry, erect or geniculate, compressed. much branched above, scabrous below panicle and usually below the glabrous nodes. Leaf sheaths compressed-keeled, glabrous or slightly scabrous on keel, ciliate on upper margin, the collar glabrate; ligule densely ciliate, 1 mm. or less long; blades mostly flat, 5–15(20) cm. long, 2–4(5) mm. wide, scabrous above, smooth or slightly scabrous beneath. Panicle spikelike, 2–6(8) cm. long, somewhat tapering above but not attenuate, occasionally interrupted or lobed below, the axis angled, scabrous, puberulent; the branches less than 3 mm. long. Bristles usually solitary below each spikelet, 3–10 mm. long, soft, antrorsely scabrous. Spikelets 1.9–2.1 mm. long; first glume about ½ as long as the spikelet, 3-nerved; second glume about ¾ as long as the spikelet, 5-nerved; sterile lemma 5-nerved, about equalling the finely but distinctly cross-wrinkled fertile lemma; sterile

palea rudimentary or up to ½ as long as the narrowly ovate fertile palea. Chromosome number $2n = 36$.

Distribution: This species is known only from the Rio Grande Plain of south Texas (Map 1).

Discusion: The earliest known collections of this taxon (*Wright 627 & 695* (GH), Val Verde Co., Texas 1849) were designated *S. setosa* (Swartz.) Beauv. by Scribner. This is a species having its main distribution in the West Indies.

The wiry, highly branched culms of *S. texana* do not occur in other perennial species from south Texas. These distinct characters in combination with small spikelet size, the occasionally decumbent culms, and short inflorescences may have been the basis for designating Wright's plants as *S. setosa*. On close examination, however, many additional morphological features are observed that distinguish the two species. In *S. texana* the leaves are glabrous, the culms although occasionally decumbent do not root at the nodes, the panicle is strict, spike-like, and rarely has branches over 3 mm. in length. This contrasts with *S. setosa* in which the leaves are usually pubescent, the culms frequently root at the nodes, and the panicles are usually loose with branches up to 4 cm. in length.

S. texana is further characterized by a distinctive somatic chromosome number. Examination of sixteen collections from localities throughout the range of this species reveal it as a tetraploid with $2n = 36$. This is the lowest number known in the *S. macrostachya* complex and it might be speculated that *S. texana* is one of the basic species from which the higher polyploid individuals have been derived.

From numerous field observations on populations of *S. texana* two facts stand out. Individuals of this species are abundant on the sandy-loam soils of the Rio Grande Plain but are rare in the clay soils that border this area. In addition to its affinity for sandy-loam soils, *S. texana* also exhibits a definite affinity for shaded habitats. Individuals are found abundantly beneath mesquite and oak trees or in the shade of cactus clumps but are rarely found in the open areas. This is true even in areas where they are protected against grazing.

S. texana is quite variable in its over-all habit. Beneath mesquite trees, oak trees, or in the shade of cactus clumps, the species exhibits a characteristic bushy appearance. In the thick mesquite brush, however, it frequently takes on a different aspect by the extended growth of one or more of its primary culms. Such culms and their secondary branches grow up through the maze of the thicket and frequently become spindly, elongate, and highly branched, with a length two to three times those of typical plants.

Some difficulty may be encountered in distinguishing between herbarium material of *S. texana* and that of the small or depauperate specimens belonging to the polymorphic species, *S. leucopila*. Such specimens appear to

intergrade in several quantitative characters. However, field examination of many sympatric populations of *S. texana* and *S. leucopila* has failed to reveal any evidence of hybridization between individuals in these populations. It seems reasonable to conclude, therefore, that the intermediate appearance of certain herbarium specimens reflects the marked phenotypic variability of the highly polymorphic *S. leucopila*, rather than hybridization and introgression between the two entities.

As indicated above this taxon is a morphologically distinct entity characterized by the lowest chromosome number ($2n = 36$) known in the *S. macrostachya* complex. Field studies indicate that it is reproductively isolated and that it exhibits specific ecological preferences. These facts, together with the restricted distribution of the species, have led this author to conclude that *S. texana* is a valid species.

Representative specimens: UNITED STATES: TEXAS: Cameron Co.: Brownsville, *Hanson 317* (GH); Rio Hondo, *Chandler 7085* (GH, US). Hidalgo Co.: 5 mi. W. of Mission, *Tharp 51–68* (TEX). Kenedy Co.: King Ranch, *Swallen 10609* (US). La Salle Co.: Cotulla, *Morgan 10B* (TEX). Starr Co.: 2.9 mi. S.W. of Santa Elena, *Johnston 541436*. Uvalde Co.: no data, *Johnson 50–122* (TEX). Webb Co.: 6 mi. N. of Bruni, *Johnston 542018* (TEX). Willacy Co.: Sauz Ranch, *Johnston 5319.147* (TEX). Zapata Co.: New Zapata, *Tharp 541947* (TEX).

SETARIA MACROSTACHYA H. B. K., Nov. Gen. & Sp. Pl. 1: 110–111. 1815. *Chamaeraphis setosa* var. *macrostachya* (H. B. K.) Kuntze, Rev. Gen. Pl. 2: 769. 1891. *Chaetochloa macrostachya* (H. B. K.) Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 29. 1900. *Chamaeraphis macrostachya* (H. B. K.) Kuntze ex Stuck., An. Mus. Nac. Buenos Aires 11: 76. 1904. Isotype examined, (Herb. Mus., Paris). MEXICO: Guanjuato: Salamanca, *Bonpland 4202*.

Panicum macrostachyum (H. B. K.) Nees, Agrost. Bras. 251. 1829. According to Hitchcock (1920) Nees based his concept of *S. macrostachya* H. B. K. on a misidentified specimen of *S. vulpiseta* from Central America.

Chaetochloa gibbosa Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 24. 1900. *Setaria gibbosa* (Scribn. & Merr.) K. Schum., Just's Bot. Jahresber. 28: 417. 1902. The holotype was examined but the fragmentary nature of this specimen (*Berlandier 528* (GH) MEXICO: Santander to Victoria, Tamaulipas) makes identification uncertain. From the description given by Scribner for *Chaetochloa gibbosa* this author believes the collection to be a depauperate form of *S. macrostachya*.

Setaria berlandieri W. Herrm., Beitr. Biol. Pfl. 10: 56. 1910. Based on *Berlandier 2248* MEXICO: Santander to Victoria, Tamaulipas. Also cited is *Palmer 505* from near Torreon, Coahuila, Mex. This latter specimen has been examined (US) and is typical *S. macrostachya*. *Chaetochloa gibbosa* and *Setaria berlandieri* are both based on collections by Berlandier from the

same locality and it may be that the two collections represent duplicate material. On the sheet of *Berlandier 528* (GH) there appear three separate numbers, *528*, *828*, and *2248*.

Description: Perennial, 60–120 cm. tall. Stems robust, erect or geniculate, compressed, rarely branched above, scabrous below the panicle and nodes. Leaf sheaths compressed-keeled, glabrous, loose, usually scabrous on the keel, ciliate along the margins, the collar glabrate; ligule densely ciliate, 2–4 mm. long; blades mostly flat, 15–20 cm. long, (0.7)1.0–1.5 cm. wide, scabrous on both surfaces, or rarely smooth beneath, generally with a few white hairs toward the base. Panicle densely flowered, 10–30 cm. long, 1–2 cm. in diameter, strict, cylindrical, or slightly tapered to the apex, occasionally interrupted or lobed below, the axis angled, scabrous, sparingly villous and puberulent, branches short. Bristles usually solitary below each spikelet, 10–20 mm. long, soft, antrorsely scabrous. Spikelets 2.0–2.3 mm. long, ovate, gibbous; first glume about 1/3 to ½ as long as the spikelet, 3–5-nerved; second glume 2/3 to ¾ as long as the spikelet, 5–7-nerved; sterile lemma 5-nerved, as long as the strongly cross-wrinkled fertile lemma; sterile palea as long as the convex, ovate, fertile palea. Chromosome number $2n = 54$.

Distribution: This species has a wide distribution and is sympatric over much of its range with *S. leucopila*. It appears to be relatively abundant throughout much of south Texas, southern Arizona, and in the state of Chihuahua, Mexico. It is also infrequent to abundant in scattered localities throughout the highlands of central Mexico (Map 2).

Discussion: The short gibbous spikelets, the convex fertile palea, the long lanceolate sterile palea ,and the robust nature of the plant, set *S. macrostachya* (*sensu stricta*) apart morphologically from any other species of the southwestern United States or northern Mexico.

In south Texas mixed populations of *S. macrostachya, S. leucopila* and *S. texana* occur. Careful examination of many such populations failed to reveal any evidence of intergradation or hybridization between these latter two species and *S. macrostachya*. In northern Mexico a few populations of a more or less intermediate nature were found. However, each was quite homogeneous in character and appeared geographically isolated from other populations of the *S. macrostachya* complex. Such intermediate plants are probably not recent hybrids or hybrid derivatives, although it is possible that they represent progeny from an ancient cross to *S. leucopila*, perpetuated by apomictic reproduction. *S. macrostachya* (*sensu stricta*) is morphologically distinct, reproductively isolated, and appears to warrant recognition as a species.

Representative specimens: MEXICO: BAJA CALIFORNIA: Cerro de la Giganta, *Carter 2086* (US). CHIHUAHUA: 65 mi. N. Chihuahua, *Emery 421* (TEX). DURANGO: Durango, *Palmer 872* (US). QUERETARO: Queretaro, *Hitchcock 5808* (US). SONORA: Canon de la Mescalera, *Santos 2115* (SMU, US); Guaymas, *Palmer 53* (US). UNITED STATES: ARI-

ZONA: Pima Co.: Sells, *Peebles 305* (US); Mt. Baboquivari, *Gould 2694* (US). Santa Cruz Co.: Patagonia, *Hitchcock 3660* (US). TEXAS: Brooks Co.: Near Falfurrias, *Emery 567* (TEX). Dimmit Co.: Asherton, *Gould 5787* (SMU). Jim Wells Co.: 15 mi. S. Alice, *Emery 568* (TEX). Kleberg Co.: Kingsville, *Swallen 10252* (US).

SETARIA LEUCOPILA (Scribn. & Merr.) K. Schum., Just's Bot. Jahresber. 28: 417. 1902. *Chaetochloa leucopila* Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 26. 1900. Isotype examined, (GH) MEXICO: Coahuila: Parras, *Palmer 1363* (1880).

Chaetochloa rigida Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 30. 1900. *Setaria rigida* (Scribn. & Merr.) K. Schum., Just's Bot. Jahresber. 28: 417. 1902. Isotype examined, (GH) MEXICO: Baja California: La Paz, *Palmer 125* (1890).

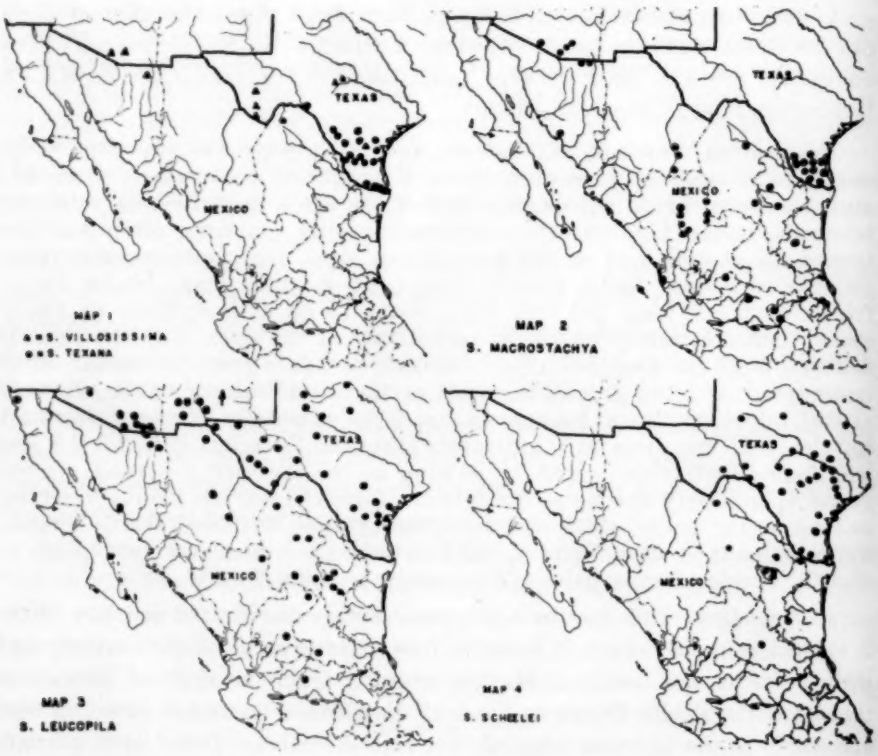
Description: Perennial, 20–100 cm. tall, usually pale or glaucous. Stems compressed, erect or geniculate from a caespitose base, rarely branched above, scabrous below the paniele and nodes, often more or less pubescent below the nodes. Leaf sheaths compressed-keeled, glabrous, often scabrous toward the summit and on the keel, villous along the upper margin, collar glabrate to hispid; ligule densely ciliate, 1.0–2.5 mm. long; blades flat or folded, 8–25 cm. long, 2–5 mm. wide, scabrous on both surfaces or nearly smooth beneath, rarely pubescent, acuminate at the apex. Panicles densely flowered, 6–15 cm. long, 1.0–1.5 cm. in diameter, pale green, columnar, often interrupted or lobed below, tapering at the apex but not attenuate, axis angled, pilose or villous; branches short. Bristles usually solitary below each spikelet, 4–15 mm. long, soft, antrorsely scabrous. Spikelets (2.1)2.2–2.5 mm. long, pale; first glume about ½ as long as the spikelet, 3-nerved; second glume ¾ to nearly as long as the spikelet, 5-nerved; sterile lemma 5-nerved, as long as the acute, short apiculate, finely cross-wrinkled fertile lemma; sterile palea lanceolate, ½ to ¾ the length of the ovate-lanceolate, plane or slightly convex, fertile palea. Chromosome number $2n = 54$, 68 or 72.

Distribution: This species is the most widely distributed member of the *S. macrostachya* complex. It is common over large areas of the southwestern United States and northern Mexico, ranging from the Gulf of Mexico on the east to the Pacific Ocean on the west. Northward it extends into Colorado and south to the Mexican state of San Luis Potosi. In Texas, it is particularly abundant south and west of the Colorado River but rare to the north and east of this line (Map 3).

Discussion: This species is a large, widely distributed, heterogeneous assemblage of several morphologically different populations. Taken individually, each of its populations is relatively homogeneous. Taken together, however, the phenotypic variability of one population over-laps that of two or more others, and their separation on morphological characters becomes difficult. In the course of the present study it became apparent that this taxon could be sub-divided into several categories on the basis of morphological criteria, but the presence of apomixis in this species signals that

caution should be exercised in attributing systematic significance to morphological variations.

The separation and recognition of *S. texana* and *S. macrostachya* (*sensu stricta*) as morphologically distinct entities necessitate the application of another name to the remaining populations formerly included in *S. macrostachya* (*sensu* Hitchcock). Fortunately, there was available in the literature a valid name, *S. leucopila* (Scribn. & Merr.) K. Schum., which was originally applied to a small, more or less atypical segment of the popula-



tions circumscribed above. This name has been adopted and to characterize more clearly the broadened concept of *S. leucopila*, a number of representative specimens of the more typical, widespread, commonly encountered populations of the group, have been cited.

Chromosome counts of approximately 33 collections of this species from Texas, New Mexico, and Arizona revealed that at least three chromosome forms occur in this species ($2n = 54$, 68, and 72). The 68- and 72-chromosome forms were found only in south Texas, whereas the 54-chromosome form occurred throughout a large portion of the species range. When ovules of this latter group ($2n = 54$) were examined, six of eight collections were

discovered to have aposporous embryo sac development. A study of the chromosome number in endosperm of these plants revealed a 5*n* condition. This is interpreted to mean that the aposporous embryo sacs by pseudogamous development of the embryo give rise to apomictic progeny. One clone of the 68-chromosome form also is known to be agamospermous. On the basis of this evidence it is assumed that apomixis is an important factor in the reproduction of this species.

There is need for a much more extensive survey of the chromosome numbers in *S. leucopila* and an attempt should be made to correlate the morphological types with the chromosome forms. Lacking such information, no useful purpose would seem served by attempting to split off additional taxa. It is the conclusion of this author that the separation of *S. macrostachya* (*sensu* Hitchcock) into *S. texana*, *S. macrostachya* (*sensu stricta*), and *S. leucopila* will facilitate and clarify future studies in this polymorphic complex.

Representative specimens: MEXICO: CHIHUAHUA: Near Chihuahua, *Le Seuer 2005* (GH, TEX). COAHUILA: Saltillo, *Hitchcock 5634* (US). GUANAJUATO: Rincon, *Sohns 470* (US). SONORA: Near Colonia Morelos, *Santos 2044* (SMU). UNITED STATES: ARIZONA: Coconino Co.: Havasupai Canyon, *Clover 4396* (SMU). Pima Co.: Near Tucson, *Harrison 8009* (SMU). COLORADO: Baca Co.: Carrizo Canyon, *Porter 4296* (US). NEW MEXICO: Chaves Co.: Frasier, *Waterfall 6144* (SMU). Dona Ana Co.: Mesilla Valley, *Fosberg S3518* (SMU); Las Cruces, *Wooton 1081* (US). Lea Co.: Lovington, *Chase 40114* (SMU). TEXAS: El Paso Co.: Hueco Tanks, *Waterfall 6629* (SMU). Kenedy Co.: El Toro Island, *Tharp 49045* (TEX, US). La Salle Co.: Cotulla, *Shinners 17283* (SMU). Loving Co.: Mentone, *Warnock 10680* (SMU). Pecos Co.: Fort Stockton, *Cory 51938* (SMU). Reeves Co.: Near Pecos, *Turner 952* (SMU).

SETARIA SCHEELEI (Steud.) Hitchc., Proc. Biol. Soc. Wash. 41: 163. 1929. *Setaria polystachya Scheele*, Linnæa 22: 339. 1849. Not *S. polystachya* Schrad. *Panicum scheelei* Steud., Syn. Pl. Glum. 1: 51. 1854. *Chaetochloa polystachya* (Scheele) Scribn. & Merr., U. S. Dept. Agr., Div. Agrost. Bull. 21: 37. 1900 *Chateachloa scheelei* (Steud.) Hitchc., Contrib. U. S. Nat. Herb. 22: 207. 1920. Isotype examined, (US) TEXAS: Comal Co.: New Braunfels, *Lindheimer 564*, 1846.

Description: Perennial, (30)60–120 cm. tall. Stems robust, usually geniculate, compressed below, occasionally branched above, scabrous below the panicle and nodes, often appressed-pilose at the nodes. Leaf sheaths compressed-keeled, glabrous, or scabrous toward the summit and on the keel, sometimes hispid on the surface, the collar hispid; ligule densely hispid, 1–2 mm. long; blades flat, (10)15–25 cm. long, pale green, loose, tapering from near the base, occasionally columnar, axis angled, scabrous-pubescent and sparsely villous; branches short to as much as 3 cm. long. Bristles usually solitary below each spikelet, 1.0–3.5 cm. long, occasionally two or more by

abortion, soft, antrorsely scabrous, spreading. Spikelets 2.2–2.5 mm. long, pale; first glume about ½ the length of the spikelet, 3-nerved; second glume ¾ to nearly as long as the spikelet, 5-nerved; sterile lemma, 5-nerved, as long as the acute, short-apiculate, incurved, finely cross-wrinkled fertile lemma; sterile palea lanceolate, about ½ the length of the ovate-lanceolate or lanceolate, plane, fertile palea. Chromosome number $2n = 54$.

Distribution: This species is common throughout central Texas. It is less common southward to the Rio Grande and into the northeastern part of Mexico. In these latter areas populations are usually limited to the alluvial soils of canyons and river bottoms. *S. scheelei* is usually observed in great abundance along the base of the Edwards Plateau where it is frequently the dominant grass in shaded areas. The escarpment of this limestone plateau runs roughly from Austin, southwest to San Antonio, and from there westward to the Rio Grande River. The numerous canyons, draws and valleys that penetrate into the plateau are particularly suited to *S. scheelei*. In such places it grows in great profusion and presents the typical growth form from which the present description was drawn (Map 4).

Discussion: This species, as a result of numerous field observations and a comprehensive study of its morphological features, was found to need some modification in its description.

Preliminary field observations indicated a remarkable similarity between the normal spike-like inflorescence of *S. leucopila* and some of the secondary inflorescences of *S. scheelei*. Further exploration located several populations in which the characteristic ". . . loose, tapering panicle . . ." of *S. scheelei* was completely absent. Close examination of such plants, however, revealed several morphological characters which indicated their close relationship to *S. scheelei*, i.e., the geniculate culms, the broad, flat, pubescent leaves, and the long, spreading bristles of the inflorescence. On the basis of numerous field observations and a comprehensive morphological examination of many herbarium specimens, these forms are interpreted to be within the phenotypic variability of *S. scheelei*. To prevent future confusion, the description of panicle shape has been amended to read ". . . loose, tapering from near the base, occasionally columnar, . . .". It is felt that this qualification serves to clarify the species limits as well as to place more emphasis on the need for using a combination of characters in the identification of this species.

Cytological observations tend to support this interpretation. In typical specimens of *S. scheelei* ($2n = 54$), as well as in those with spike-like panicles, meiotic divisions are completely regular and pollen fertility is high. This contrasts with the known 54-chromosome forms of *S. leucopila* in which the chromosomes are completely asynaptic in the meiotic division, the anaphase separation is frequently unequal, the second meiotic division is often omitted, and the pollen fertility is low.

At many points along the base of the Edwards Plateau and in a few

areas of south Texas populations of *S. scheelei* have been observed in close association with others of *S. leucopila*. The lack of hybridization and introgression in areas of this type has led the writer to conclude that *S. scheelei* is reproductively isolated from *S. leucopila*. The relationship of *S. scheelei* to *S. villosissima* in terms of reproductive isolation is not known but the discontinuity in spikelet size between these two species is so complete as to indicate that little if any introgression is taking place between the two entities.

Representative specimens: MEXICO: COAHUILA: Cuatro Cienegas, *Marsh 2027* (US). NUEVO LEON: Monterrey, *Pringle 1968* (US). SAN LUIS POTOSI: Cardenas, *Hitchcock 732* (GH, US). TAMAULIPAS: Near El Rosario, *Bartlett 10867* (GH). UNITED STATES: TEXAS: Bell Co.: Little River, *Wolff 1013* (US). Bexar Co.: San Antonio, *Emery 584* (TEX). Cameron Co.: Brownsville, *Runyon 1894* (US). Live Oak Co.: Near George West, *Shinners 17005* (SMU). McLennan Co.: Waco, *Shinners 16686* (SMU). Mills Co.: Near Goldthwaite, *Cory 58214* (SMU). San Saba Co.: Near San Saba, *Cory 58300* (SMU). Uvalde Co.: Near Uvalde, *Emery 589* (TEX).

SUMMARY

1. This investigation presents a taxonomic treatment of five closely related, perennial species of the genus *Setaria* from the southwestern United States and northern Mexico.

2. Evidence in the form of chromosome numbers, populational studies, and a reevaluation of morphological characters has been presented to support the interpretation that *S. macrostachya* H.B.K. (*sensu* Hitchcock) should be separated into three distinct species; *S. texana* sp. nov., *S. macrostachya* H.B.K. (*sensu stricta*) and *S. leucopila* (Scribn. & Merr.) K. Schum.

3. Similar evidence has been applied in clarifying the species limits of *S. scheelei* (Steud.) Hitchc. and *S. villosissima* (Scribn. & Merr.) K. Schum.

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A STUDY OF REPRODUCTION IN SETARIA MACROSTACHYA AND ITS RELATIVES IN THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO[1]

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The genus *Setaria* is a relatively small genus of approximately sixty-five species distributed throughout the tropical and warm temperate regions of both hemispheres. From an economic standpoint it is perhaps best known through the agriculturally important *Setaria italica* (L.) Beauv., or foxtail millet. There are, however, several other species in this genus with considerable economic importance.

Recently certain perennial, closely related, polyploid forms native to the southwestern United States and northern Mexico have received appreciable attention because of their importance as forage and range cover in these arid and semi-arid regions. Certain forms are common, widespread, and extremely variable; others are rare, relatively homogeneous, and restricted in their distribution.

In the present study these grasses are designated as comprising the *Setaria macrostachya* complex. The systematics of this complex are treated in a separate paper (Emery 1957) and include the following species: *S. macrostachya* H. B. K. (*sensu stricta*), *S. leucopila* (Scribn. & Merr.) K. Schum., *S. texana* Emery, *S. villosissima* (Scribn. & Merr.) K. Schum., and *S. scheelei* (Steud.) Hitchc.

The terminology and literature dealing with the phenomena of apomixis have been thoroughly reviewed and discussed by Stebbins (1941), by Gustafsson (1946, 1947a and b), and by Nygren (1954). The reader is referred to these papers for a critical treatment of the subject. In the present paper the simplified terminology as proposed and defined by Gustafsson (1946) is adopted.

Agamospermy, or the production of seed without fertilization, has been reported in several families of the angiosperms (Gustafsson 1946, 1947a and b; Nygren 1954). In the grass family 33 species of 11 genera have been reported to reproduce in this manner. Table 1 lists the distribution of agamospermy in tribes and genera of the Gramineae, the type of apomixis, and the number of agamospermous species reported from each genus.

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TABLE 1. *Agamospermy in the Gramineae.* (*A* = *apospory; D* = *diplospory; P* = *parthenogenesis*).

Tribe	Genus	Number of species	Type of apomixis
Festuceae	*Poa*	11	D, P & A, P
Agrostideae	*Calamagrostis*	7	D, P
Chlorideae	*Bouteloua*	1	A, P
Paniceae	*Cenchrus*	1	A, P
	Paspalum	1	A, P
	Panicum	1	A, P
	Pennisetum	5	A, P
	Setaria	2	A, P
Andropogoneae	*Andropogon*	1	A, P
	Saccharum	2	D, P
Tripsaceae	*Tripsacum*	1	?, P

Recent investigations in the tribe Paniceae have revealed several cases of apomictic reproduction in which apospory is followed by parthenogenesis. Smith (1948) reported the production of aposporous embryo sacs followed by an autonomous development of the embryo in *Paspalum dilatatum* Poir. Later Narayan (1951) in a broad survey of the reproductive processes in *Pennisetum* observed the production of aposporous embryo sacs in certain strains of *P. villosum* R. Br., *P. setaceum* (Forsk.) Chiov., *P. orientale* Link and *P. clandestinum* Hochst. ex Chiov. Embryo development in *P. clandestinum* was pseudogamous while that in the remaining three species was reported to be autonomous. Evidence was also reported indicating a tendency toward apospory in *P. ramosum* C. Sm. Fisher, Bashaw and Holt (1954) and Snyder, Hernandez and Warmke (1955) reported apomixis in *P. ciliare* (L.) Link and in *Cenchrus setigerus* Vahl. The latter authors noted that the apomictic mechanism in these two species involved the formation of one or more aposporous, four-nucleate embryo sacs. Removal of stigmas from ovules in two strains of *P. ciliare* prior to anthesis effectively prevented development of the embryo, while the controls set abundant seed. This indicates a pseudogamous development of the embryo. Warmke (1954) observed in four strains of *Panicum maximum* Jacq. that aposporous, four-nucleate embryo sacs were formed, followed by pseudogamous development of the embryo. Unpublished data of W. V. Brown and the writer indicate that aposporous, four-nucleate embryo sacs also occur in several other species of grasses.

The object of the present investigation was to characterize the cytological aspects of the species in the *S. macrostachya* complex. It includes a survey of the somatic chromosome numbers and a careful study of the mechanism of reproduction in each species.

Materials and methods. Many of the collections used in this study were obtained from permanent plantings in an experimental plot. Others were

made at various localities throughout a large portion of Texas. To avoid loss of collections and to provide a check of the effects of greenhouse culture on the plants, each collection was split; one part of the clone was grown in the experimental plot and one part was potted and grown in the greenhouse.

The somatic chromosome number of each collection has been determined from root-tip smears. Root-tips were pretreated 2–3 hrs. in a 0.002 M. solution of 8-hydroxyquinoline, stained and hydrolyzed in a 9:1 solution of two per cent aceto-orcein and N HCl, and smeared in a one per cent aceto-orcein solution (Tjio & Levan 1950).

Cytological studies of microsporogenesis and megasporogenesis were made primarily of material collected from plants grown in the greenhouse, but an examination of small samples from field grown material of the same clones showed no significant variation in the cytological aspects. Materials were prepared for the study of microsporogenesis by the standard aceto-carmine smear technique, while for the study of megasporogenesis, sectioned material stained in Delafield's hematoxylin was used.

The endosperm in several collections was studied in an effort to determine if the functional embryo sacs were sexual or if they were produced by some form of apomixis. Endosperm in the sexual embryo sacs of most grasses is triploid and is formed by the fusion of two reduced polar nuclei with a reduced male gamete. In most apomicts characterized by apospory or by diplospory, the endosperm results from the fusion of two unreduced polar nuclei ($2n+2n$) or by the triple fusion of two unreduced polar nuclei and a reduced male gamete ($2n+2n+1n$). A $4n$ or $5n$ endosperm constitution is assumed therefore, to indicate the autonomous or pseudogamous development, respectively, of an unreduced embryo sac.

For the determination of chromosome numbers in endosperm cells, florets were selected in which the ovary had begun to enlarge but had not yet formed appreciable quantities of starch. The ovary was dissected from the floret and the ovule in turn was separated from the ovary wall. Once free of the ovary wall, ovules were stained and hydrolyzed in a warm 9:1 solution of two per cent aceto-orcein and N HCl. They were then smeared in a drop of one per cent aceto-orcein.

Pollen fertility was determined by examination of a random sample of pollen stained in a one per cent IKI solution or in a solution of cotton blue in lactophenol. The stainability and fullness of the pollen grains were taken as criteria of fertility. It is probable that in certain instances, to be cited later, such criteria are inadequate.

With the exception of a few individuals that were lost and others that died during the period of experimentation, specimens of each collection have been deposited in the herbarium of The University of Texas. The individual collections of all material utilized in this study are cited in the appendix of the author's thesis (Emery 1956).

Observations. Somatic chromosome numbers. Somatic chromosomes in members of the *S. macrostachya* complex afford little opportunity for determining species relationships by idiogram analysis. They are small, not easily stained, and vary only slightly in their over-all length (fig. 1). No distinguishing morphological characters that might aid in determining the duplication of a genome have been found.

Previous to this study only one chromosome count had been reported for the *S. macrostachya* complex. Brown (1950) reported $2n = 72$ for a plant of *S. macrostachya* H. B. K. = [*S. leucopila* (Scribn. & Merr.) K. Schum.]. Table 2 lists the $2n$ chromosome numbers and the number of collections examined for each taxon included in this study.

TABLE 2. *Somatic chromosome numbers in species of the Setaria macrostachya complex.*

Species	Number of collections counted	Number $2n$
S. leucopila		
54-chromosome form	18	54
68-chromosome form	3	68
72-chromosome form	12	72
S. macrostachya	8	54
S. texana	16	36
S. villosissima	2	54
S. scheelei	8	54

Microsporogenesis. The meiotic divisions in microsporocytes of *S. scheelei*, *S. villosissima*, and the 72-chromosome form of *S. leucopila* are completely regular. In prophase the chromosomes are observed to form bivalents which later move onto the metaphase plate and disjoin normally at anaphase. Cells of the resulting dyad undergo a normal second division to form a tetrad of spores. Pollen fertility is high (*S. scheelei* 89–98 per cent; *S. villosissima* 88–92 per cent; and in the 72-chromosome form of *S. leucopila* 88–92 per cent).

In *S. texana* and in the 68-chromosome form of *S. leucopila* there is a normal heterotypic division, resulting in the production of a dyad from each pollen mother cell. Later stages of development, however, exhibit considerable irregularity. Frequently the second division is completely omitted and the cells of the dyad are observed to develop thickened walls. These cells separate from each other and round out into partially filled pollen grains. When a second division occurs, there is usually distortion of the spindles causing various abnormal arrangements of the tetrad. An examination of sectioned material revealed that relatively large portions of the sporogeneous tissue degenerates before the initiation of the second division. The specific cause of this degeneration is unknown, but the result is evident in the low pollen fertility of both species (*S. texana*, 12–20 per cent; and the 68-chromosome form of *S. leucopila*, 10–16 per cent).

The meiotic divisions in *S. macrostachya* ($2n = 54$) and in the 54-chromosome form of *S. leucopila* are characterized by a complete absence of paired chromosomes at the heterotypic diakinesis and metaphase I. There are, however, many diakinesis figures that show some association of the univalent chromosomes in irregular groupings. These groups involve from 2–6 units, but there is no indication that they represent or are produced by the pairing of homologous chromosome segments. The univalents of the microsporocyte usually move to the center of the cell where they form a metaphase plate. A spindle mechanism is formed and approximately half of the 54 univalent chromosomes move to each pole. It is doubtful, however, that in all cases the two chromosomes of each homologous pair go to opposite poles. Probably the resulting cells of the dyad contain various degrees of chromosome duplication and deficiency and it is assumed that this unbalanced condition accounts for a portion of the observed pollen sterility. Cytokinesis follows the nuclear division and the two cells of the dyad round up to form pollen grains. Rarely have second division figures or their derivatives been observed.

In addition to the complete asyndesis of the chromosomes, numerous other meiotic irregularities have been observed in *S. macrostachya* and in the 54-chromosome form of *S. leucopila,* i.e., precocious and lagging chromosomes (fig. 2), chromosomes excluded from the spindle, stickiness of chromatin material, and the formation of micro-nuclei. The most common and probably the most important irregularity of microsporogenesis, however, is the degeneration of sporogeneous tissue at various stages in development.

As indicated in the preceding description of microsporogenesis, plants of *S. macrostachya* and the 54-chromosome form of *S. leucopila* have a more or less equal anaphase separation of the univalent chromosomes. Occasionally, however, abnormally large and abnormally small pollen grains were observed in some anthers of these plants (fig. 3). Pollen stainability in *S. macrostachya is* 5–10 per cent while that of the 54-chromosome form of *S. leucopila* is 8–15 per cent. These figures include the aberrant grains which are full of protoplasm and stain deeply, but the fertility of these is highly dubious in view of their abnormal size and the irregular meiotic division from which they are derived. A majority of the grains are neither full nor stained.

Megasporogenesis and embryo sac development. In the study of megasporogenesis a total of 28 plants have been examined. The numerical distribution of these collections is as follows: *S. leucopila* 12, *S. macrostachya* 5, *S. texana* 4, *S. villosissima* 2, and *S. scheelei* 5.

Differentiation of the primary archesporial cell is essentially the same as that described for other closely related grasses such as *Panicum maxi-*

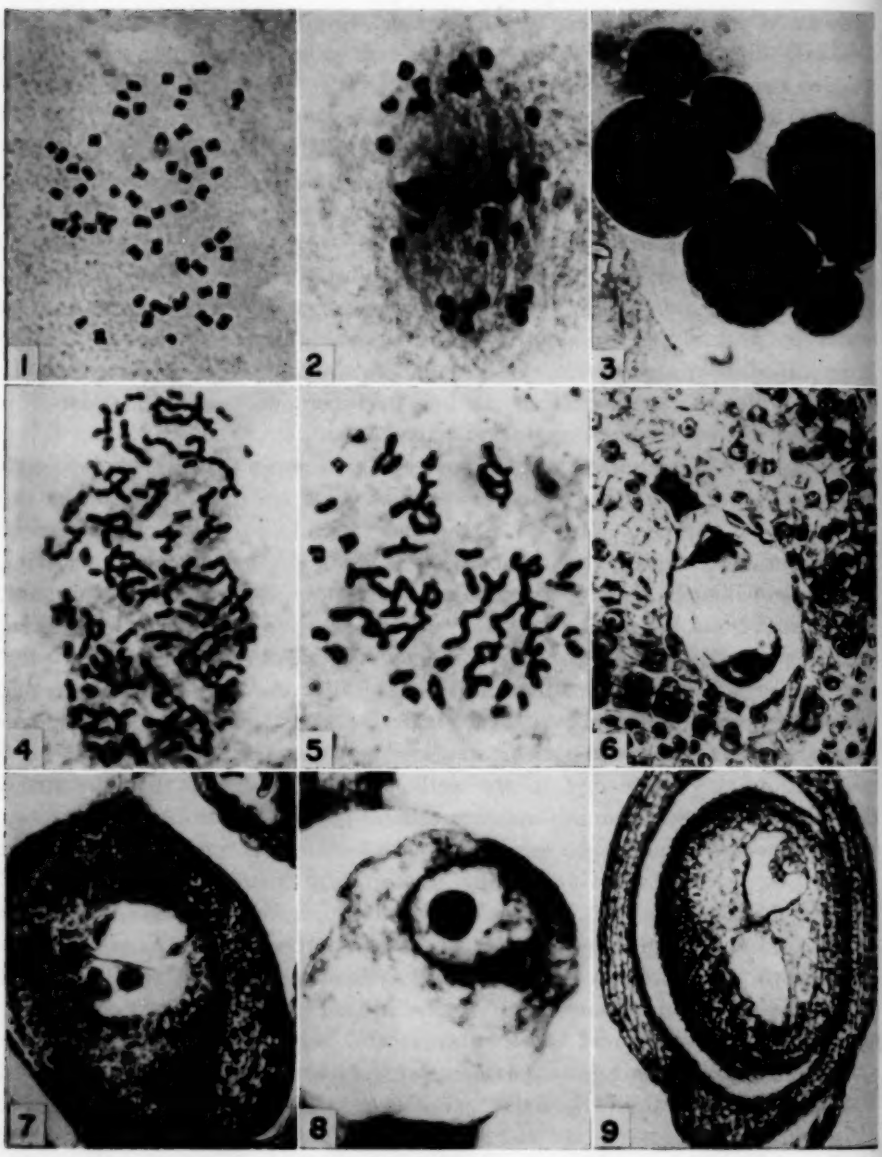
mum and *Pennisetum ciliare* (Warmke 1955, Snyder, Hernandez & Warmke 1955). Following enlargement and elongation of the archesporial cell a nuclear division is initiated.

The first division of the megasporocyte occurs at approximately the same time as the first division of the microsporocyte. In *S. scheelei, S. villosissima, S. texana,* and in the 68- and 72-chromosome forms of *S. leucopila* the chromosomes pair normally and move onto the metaphase plate. Because of the difficulty in obtaining division figures of the subsequent stages in megasporogenesis the picture is somewhat fragmentary. Chromosomes of *S. scheelei, S. texana,* and the 68-chromosome form of *S. leucopila* appear to undergo a normal first meiotic division. Division figures of the megasporocyte in *S. villosissima* and the 72-chromosome form of *S. leucopila* were not observed. Following completion of the first division, cytokinesis is initiated in each case to produce a characteristic dyad.

Many of the irregularities of microsporogenesis in *S. macrostachya* and in the 54-chromosome form of *S. leucopila* were also observed in the development of the megaspores, i.e., complete asyndesis of the chromosomes, precocious and lagging chromosomes, stickiness of the chromatin material, and the occasional degeneration of the megasoporocyte in early prophase. In spite of these irregularities the two halves of a dividing megasporocyte appear to contain a more or less equal amount of chromatin material and are separated by a cell wall. As mentioned earlier under microsporogenesis, it seems probable that the two chromosomes of each homologous pair do not always move to opposite poles, creating various degrees of chromosome duplication and deficiency in the cells of a dyad. Such an unbalanced chromosome condition may well explain a portion of the observed seed sterility in *S. macrostachya* and in the 54-chromosome form of *S. leucopila* (Table 5).

In *S. villosissima* and in *S. scheelei* the two cells of the dyad were observed to divide simultaneously to form a tetrad of spores. In *S. villosissima* this tetrad is crushed by the enlarging aposporous embryo sacs, while in *S. scheelei* the three spores nearest the micropylar end of the ovule degenerate and the chalazal spore enlarges and becomes vacuolate. In other species of the *S. macrostachya* complex, however, the micropylar spore usually degenerates shortly after completion of the first meiotic division. Following a short interphase, the remaining cell of the dyad divides to form two spores and the one nearest the micropylar end of the ovule degenerates rapidly. The chalazal spore enlarges and becomes highly vacuolate as in *S. scheelei.*

Development of an embryo sac from a reduced spore in both the sexual and the apomictic species of the *S. macrostachya* complex follows the pattern described for the Polygonum type embryo sac (Maheshawari 1950). Shortly



FIGS. 1–9. FIG. 1. Somatic metaphase in *Setaria leucopila* with 54 chromosomes. FIG. 2. Irregular anaphase separation of the 54 univalent chromosomes in a microsporocyte of *Setaria leucopila*. FIG. 3. Abnormally large and small pollen from anthers of the 54-chromosome form of *Setaria leucopila*. FIG. 4. Division of an endosperm nucleus showing approximately 135 chromosomes ($5n$), 54-chromosome form of *Setaria leucopila*. FIG. 5. Division of an endosperm nucleus showing approximately 81 chromosomes ($3n$), *Setaria scheelei*. FIG. 6. A partially degenerate, two-nucleate sexual embryo sac with a dnesely cytoplasmic aposporous embryo sac initial at the chalazal end,

after completion of the third nuclear division the eight-nucleate embryo sac organizes into an egg, two synergids, two polar nuclei, and three antipodals. Before fertilization it is common for the antipodals to undergo further nuclear and/or cell division in a manner which is typical of grasses (Brown 1949).

Apospory. Seven plants of *S. leucopila* and two of *S. villosissima* were observed to form one or more aposporous embryo sacs in the majority of ovules studied. Six of the seven plants of *S. leucopila* belong to the 54-chromosome form, while the remaining plant belongs to the 68-chromosome form.

Indications of apospory were not usually apparent until the sexual embryo sac was in the two to four-nucleate stage. At that time a cell of the nucellus adjacent to the reduced tissue took on an intense cytoplasmic stain (fig. 6), enlarged, and became highly vacuolate. Where it was possible to observe the formation of the initial aposporous embryo sac it was always in contact with some portion of the reduced tissue. Subsequent formation of additional aposporous embryo sacs seems to be possible by any cell of the nucellar or chalazal region of an ovule, except those of the epidermis. As many as eight have been observed within a single ovule.

The frequency of aposporous embryo sac formation varies greatly from clone to clone, but the characteristic pattern of aposporous development is the same in each of the nine apomictic collections. As the aposporous embryo sac initial approaches completion of its enlargement small vacuoles at the chalazal end of the cell appear to coalesce, causing the nucleus and most of the cytoplasm to become situated at the micropylar end. This is the common situation, since most of the embryo sacs form in the micropylar end of the ovule, but where they develop in the chalazal region the nucleus comes to lie in the end of the cell closest to the surface of the ovule. Following a short period, two nuclear divisions occur in quick succession. The first is usually oriented more or less at right angles to the long axis of the cell. It is followed by a second division to give a four-nucleate embryo sac. All four of the nuclei remain in the lower end of the embryo sac where they may or may not become further differentiated. Subsequent organization of the aposporous embryo sacs in *S. villosissima* and in the 54- and 68-chromosome forms of *S. leucopila* produces an embryo sac with one egg, one synergid, and two polar nuclei (fig. 7).

Within many ovules aposporous embryo sac initials continue to form in spite of the presence of one or more mature, fully organized sacs. Just as

54-chromosome form of *Setaria leucopila*. FIG. 7. Four-nucleate aposporous embryo sac organized into one egg, one synergid and two polar nuclei, *Setaria villosissima*. FIG. 8. Egg cell with a large egg nucleus and a smaller male nucleus lying against it, 54-chromosome form of *Setaria leucopila*. FIG. 9. Four-nucleate aposporous embryo sac with the egg-apparatus oriented toward the chalazal end of the ovule, *Setaria villosissima*.

TABLE 3. *Sporogenesis and embryology in species of the Setaria macrostachya complex.*

Species	Microsporogenesis		Megasporogenesis		Sexual embryo sac	Aposporic embryo sac
	1st Division	2nd Division	1st Division	2nd Division		
S. leucopila						
54-chrom. form	Asyndesis	Occasionally present	Asyndesis	Frequently absent	Polygonum type	4-nucleate type
68-chrom. form	Regular	Frequently absent	Regular	Frequently absent	Polygonum type	4-nucleate type
72-chrom. form	Regular	Regular	Regular	Regular	Polygonum type	None observed
S. macrostachya	Asyndesis	Occasionally present	Asyndesis	Frequently absent	Polygonum type	None observed
S. texana	Regular	Frequently absent	Regular	Occasionally absent	Polygonum type	None observed
S. villosissima	Regular	Regular	Regular	Regular	None observed	4-nucleate type
S. scheelei	Regular	Regular	Regular	Regular	Polygonum type	None observed

the initial aposporous embryo sac enlarges and encroaches upon the sexual embryo sac, so the successively-formed aposporous sacs enlarge and encroach upon each other. The formation of numerous embryo sacs and their mutual crushing or abortion results, occasionally, in the destruction of the entire nucellus and a sterile ovule results. A more common occurrence is the formation of one or two aposporous embryo sac initials close to the sexual embryo sac and an additional one in a chalazal portion of the nucellus. The aposporous embryo sac or sacs adjoining the sexual one may or may not crowd out the latter, while the embryo sac in the chalazal portion of the ovule develops to maturity without competition. Ovules at the time of fertilization were observed in the following conditions: (1) one or more unreduced aposporous sacs, (2) one reduced and one aposporous embryo sac, (3) one reduced embryo sac or (4) a sterile ovule with no functional embryo sac. A general summary of sporogenesis and embryo sac formation is presented in Table 3.

Mature aposporous embryo sacs occurring in the chalazal portion of an ovule are usually organized with the egg apparatus oriented toward the nearest surface of the ovule (fig. 9). A similar condition has been reported by Snyder, Hernandez & Warmke (1955) in the four-nucleate embryo sacs of *Pennisetum ciliare*. Although the four-nucleate embryo sacs in the chalazal portion of the ovules of *S. villosissima* and *S. leucopila* may develop to maturity they seldom if ever function in the production of an embryo. Usually one of the embryo sacs in the micropylar portion of the ovule functions in this capacity. No case of polyembryony was observed in any of the present material.

Development of the endosperm and embryo. Fertilization within the eight-nucleate sexual embryo sac appears to be effected in a normal manner, with one male gamete fertilizing the egg and the second male gamete entering into a triple nuclear fusion with the two polars. Examination of endosperm smears from ovules of *S. scheelei*. (fig. 5) and *S. texana* revealed a $3n$ chromosome constitution, characteristic of other sexually reproducing grasses.

In the aposporous embryo sacs the pollen tube enters through the synergid discharging two male gametes into the unreduced embryo sac. One of these male gametes enters into a triple fusion with the two unreduced polar nuclei, while the second male gamete may or may not enter the egg cell. In either case, the unreduced egg nucleus of an aposporous embryo sac is not fertilized. Endosperm smears prior to the formation of starch reveal that nuclei of this tissue contain the $5n$ chromosome number (fig. 4). Endosperm from five apomictic plants of *S. leucopila* has been examined and in each case the $5n$ chromosome constitution of the nuclei was confirmed.

In one endosperm smear from an apomictic plant of *S. leucopila* several

cells were counted in which the chromosome constitution approximated a $3n$ condition. This has been interpreted as evidence for the occasional development of a sexual embryo sac in ovules of the apomictic plants. Such an interpretation is further supported by the fact that, occasionally, in sectioned material, persisiting antipodal cells can be observed at the chalazal end of the developing endosperm. These cells are not known to occur in aposporous embryo sacs of *Setaria* and, therefore, their presence in an apomictic plant is assumed to indicate the occasional development of a sexual embryo sac. Such plants would, of course, be facultative apomicts.

Tests to confirm the interpretation of pseudogamous development of the embryo by emasculation or stigma removal were not considered feasible because of the irregular anthesis of florets over the densely-flowered, spike-like inflorescence. In *S. texana* and in certain collections of *S. macrostachya* there was the added difficulty of cleistogamous development of florets.

The partially indurate fertile lemma and palea in spikelets of *S. texana* and *S. macrostachya* frequently fail to open, and the flower is assumed to be self-pollinated. By careful dissection of the lemma and palea from fertile florets it was possible to demonstrate the frequent presence of three anthers and a complete stigma impressed in the surface of the enlarging ovary. Examination of sectioned material also revealed fertile florets in which the anthers and stigma had failed to exsert. The possibility that the cleistogamous development of florets might be the result of environmental conditions in the greenhouse was also checked. Mature florets from several herbarium specimens were removed and by dissection of the fertile lemma and palea from the floret it was possible to demonstrate the unexserted anthers and stigma impressed on the surface of the ovary.

In plants producing aposporous embryo sacs several cases have been observed in which the male gamete entered the egg cell but the nuclei failed to fuse (fig. 8). The relatively high frequency of such nuclear associations in apomictic plants, together with the $5n$ constitution of the endosperm nuclei are interpreted as additional evidence for the pseudogamous development of the embryo in plants of *S. leucopila*. It is unlikely that there is a fusion of the unreduced egg nucleus and the reduced male nucleus, since, in a study of somatic chromosome numbers in progenies from apomictic plants, variations in the chromosome number were not detected.

The initial division of the pro-embryo occurs while the endosperm is still in a "free nuclear" condition. The pattern of pro-embryo development is the same for *S. scheelei* (sexual) and for the apomictic embryos in *S. leucopila*. It follows the general scheme of grass embryo development described for *Poa annua* by Soueges (1924).

Progeny tests. Small scale progeny tests of two of the aposporous clones of *S. leucopila* provide evidence that these are facultatively apomictic. In

progeny from one plant, two of 24 individuals were aberrant with respect to leaf color and the over-all stature of the plants. In the progeny from the second plant, one of six individuals appeared to be aberrant. Morphologically homogeneous plants from a given parent are interpreted as representing asexually reproduced individuals while the aberrants are considered to be the result of sexual reproduction. Counts of the somatic chromosomes of these aberrant plants revealed no departure from the $2n$ condition observed in the parents.

It is not known if *S. villosissima* is an obligate or a facultative apomict. The rare occurrence of obligate, agamospermous apomicts among the grasses and the close relationship of *S. villosissima* to the facultative apomict *S. leucopila* strongly suggests, however, that it may also be a facultative apomict.

In conjunction with the progeny tests on individuals of the *S. macrostachya* complex limited data relative to the seed set or number of mature caryopses produced per hundred florets was obtained. This data is presented in Table 4.

TABLE 4. *Seed set in species of the Setaria macrostachya complex.*

Species	Florets examined	Average number of caryopses per hundred florets
S. leucopila		
54-chrom. form	1800	10.3
68-chrom. form	600	23.8
72-chrom. form	5000	56.0
S. macrostachya	600	3.2
S. texana	600	60.2
S. villosissima	600	25.5
S. scheelei	600	70.2

It is evident that the sexual groups with the exception of *S. macrostachya* set a higher per cent of seed than do the plants of the apomictic groups. The low seed set of the sexual *S. macrostachya* is not surprising in view of its irregular meiotic division and the degeneration of reduced tissue which appears inherent within ovules of this species. The matter of ovule abortion will be considered further in the discussion.

Discussion. *S. leucopila* and *S. villosissima* are two more species in the rapidly increasing list of perennial grasses known to produce seed by agamospermy. Once considered to be a freak occurrence, agamospermy is now found to be relatively common and widely distributed within the grass family (see Table 1). Most of these agamospermous species of grasses are facultatively apomictic, producing seeds both sexually and asexually. The rather high frequency of facultative apomicts and their relative biological

success in specialized families such as the Compositate and the Gramineae, have led several investigators to consider the evolutionary significance of apomictic reproduction and its effect on species variability (Stebbins 1950, Clausen 1954).

Two of the more significant features observed in the present investigation are (1) sexual sterility, and (2) the production and organization of aposporous, four-nucleate embryo sacs in *S. leucopila* and *S. villosissima*.

A high degree of sexual sterility is not uncommon in many of the perennial grasses of the Southwest (Brown 1943). The cause of this sterility is not attributable to any one type of factor, and varies from species to species. In some it may be primarily a result of environmental conditions while in others sexual sterility is undobutedly the result of genic or chromosomal conditions. Brown (1943) has shown that with many perennial range grasses the seed set is directly correlated with environmental factors such as soil moisture. Genic sterility on the other hand is expressed through the failure of sex organs to develop as in dioecious plants (Jones 1931) or certain abnormalities of the meiotic process, i.e., the asynapsis or desynapsis of chromosomes (Beadle 1930; Li, Pao, and Li 1945). In the *S. macrostachya* complex there appears to be at least two distinct and probably gene-controlled factors responsible for a large portion of the observed sexual sterility (Table 5). The most striking effect results in a complete asyndesis of the chromosomes in both *S. macrostachya* and in the 54-chromosome form of *S. leucopila*. It is assumed that failure to synapse disturbs the precision of the meiotic process and results in precocious and lagging chromosomes, micronuclei, unequal anaphase I separation, abnormal arrangement of tetrads, irregular size of pollen grains, and finally in a high degree of sexual sterility. This mechanism appears to be reinforced by a second gene mechanism that effects degeneration of reduced or gametophytic tissue throughout the plant. Degeneration and abortion of young ovules is not uncommon in many interspecific hybrids (Cooper & Brink 1944 and 1945) but it is usually accompanied by hypertrophy of the maternal nucellar tissue.

No such effect has been observed in any of the material studied in the *S. macrostachya* complex. The effect as observed in *S. macrostachya* and in the 54-chromosome form of *S. leucopila* appears clearly different from the ovule abortion reported by Brink and Cooper, both in the specificity of effect and in the time of response. Brown and Coe (1951) have reported ovule abortion in two sexual species of *Hilaria* that appears similar in most respects to the degeneration of spores and gametophytic tissue observed in the present material. They found that the ovule abortion of *Hilaria belangeri* and *H. mutica* was inherent within the species and results from a degeneration of the sporogeneous or gametophytic tissue at various times following the first division of the megasporocyte.

In *S. villosissima* the mechanism responsible for sexual sterility appears to be somewhat different from that described in *S. macrostachya* and in the 54-chromosome form of *S. leucopila*. Here the development of the chalazal megaspore is arrested. Neither vacuolization of the potential embryo sac initial nor degeneration of the three micropylar spores was observed. Final degeneration of the tetrad appears to result from a physical crushing of the four spores by an enlarging aposporous embryo sac adjacent to the spores.

The production of four-nucleate embryo sacs as found in material of *S. villosissima* and in the 54- and 68-chromosome forms of *S. leucopila* is a rather unique condition. Previous workers have shown that it occurs in four species of *Pennisetum* (Narayan 1951; Snyder, Hernandez & Warmke, 1955) in one species of *Panicum* (Warmke 1954) and in one species of *Cenchrus* (Snyder, Hernandez & Warmke, 1955). In each case the aposporous four-nucleate embryo sac has been reported to be organized into two synergids, one egg, and one polar nucleus. This condition contrasts with that found in the two species of *Setaria* where the four nuclei become organized into one synergid, one egg, and two polar nuclei. As a result of this organization the endosperm nucleus of the latter type embryo sac has a higher level of polyploidy ($5n$) than those of the former type ($3n$).

The partially self-fertilized nature of two supposedly sexual species, *S. texana* and *S. macrostachya* is highly unusual when considered in the light of existing evidence from other agamic complexes. In a large majority of the agamic complexes so far reported the sexual members of such groups have been found to be self-incompatible, monoecious, dioecious, or at least usually cross-fertilized under natural conditions (Gustafsson 1947). In the agamic complex of *Calamagrostis*, Nygren (1946) reports that all the sexual species are highly self-incompatible. The work of Clausen, Keck and Hiesey (1947, 1948) has indicated that the sexual species of the thoroughly investigated *Poa* complexes are predominately cross-fertilized. Nygren (1950) however, reported a sexual species of *Poa* (*P. laxa* subsp. *flexuosa*) from Scandinavia in which the plants are predominately autogamous. Thus it would appear that sexual members of an agamic complex are usually cross-fertilized but this condition is not without exceptions.

SUMMARY

1. Five perennial species of the genus *Setaria* from the southwestern United States and northern Mexico have been investigated.

2. Cytological examination reveals that they are polyploid members of an agamic complex.

3. *S. texana* ($2n = 36$), *S. scheelei* ($2n = 54$), *S. macrostachya* ($2n = 54$), and the 72-chromosome form of *S. leucopila* reproduce sexually.

4. *S. villosissima* ($2n = 54$) together with the 54- and 68-chromosome forms of *S. leucopila* reproduce asexually by agamospermy.

5. The apomictic mechanism of these taxa usually includes the degeneration of sporogeneous or gametophytic tissue, the formation of aposporous embryo sacs, and the pseudogamous development of the embryo.

6. Two types of embryo sacs are formed, i.e., the 8-nucleate, 7-celled Polygonum type (sexual) and a 4-nucleate, 3-celled aposporous type (apomictic).

7. *S. leucopila* has been shown to be a facultative apomictic by progeny tests, by endosperm smears, and by a direct study of the megagametophyte development.

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BULLETIN OF THE TORREY BOTANICAL CLUB
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TORREYA

CONSTITUTION AND BY-LAWS OF THE TORREY BOTANICAL CLUB

(Revised, DECEMBER, 1956)

CONSTITUTION

ARTICLE I NAME

The name of this Society shall be The Torrey Botanical Club.

ARTICLE II OBJECTS

The objects of the Club shall be to collect and diffuse information on all topics relating to botany and to promote an interest in this science.

ARTICLE III OFFICERS

The officers of the Club shall consist of a President, a Vice-President, a Treasurer, a Corresponding Secretary, a Recording Secretary, an Editor, a Manager of Publications, a Bibliographer, and an Historian. The officers shall be elected annually by ballot, and shall hold their offices for one year, or until others are installed in their places.

Vacancies occurring in any of the offices of the Club shall be filled by election by the Council. The person so elected shall serve until the next annual election, or until a successor is chosen.

ARTICLE IV PRESIDENT

The President shall preside at all meetings of the Club and Council, and shall appoint all committees not otherwise provided for.

ARTICLE V VICE-PRESIDENT

In the absence or disability of the President, his duties shall be performed by the Vice-President, and in the absence or disability of the latter, another officer shall serve, the order of precedence being that indicated in Article III.

ARTICLE VI TREASURER

The Treasurer shall collect and have charge of all funds and securities of the Club. Out of such funds he shall pay the ordinary current expenses of the Club and such other sums as may from time to time be ordered. He shall report to the Council all members three months in arrears for dues. No payment exceeding twenty-five dollars ($25.00) shall be made by the Treasurer, except as authorized by the Annual Budget, unless first approved by the Council. The Treasurer's books shall be audited at least once every year by an Auditing Committee appointed for that purpose. The Treasurer shall render a report of the finances of the Club at the Annual Meeting, or oftener if requested, and at any other time he may desire.

ARTICLE VII SECRETARIES

The Corresponding Secretary shall have charge of the Charter, Seal, Constitution, and By-laws of the Club. He shall give due notice of all meetings, conduct the correspondence of the Club, and prepare all letters to be written in its name, retaining copies of them. He shall serve as Chairman of the Program Committee and of the Publications Exchange Committee, and perform such other duties of a similar nature as may be assigned by the Club from time to time.

The Recording Secretary shall keep full and accurate records of the membership

and proceedings of the Club and Council, receive all applications for membership, notify each member of his election, and report to the Treasurer the name and residence of each member elected, and perform such other duties of a similar nature as may be assigned by the Club from time to time.

Article VIII Editor

The Editor shall have final editorial authority over all publications of the Club and appoint Associate Editors subject to the approval of the Council.

Article IX Manager of Publications

The Manager of Publications shall collect and turn over to the Treasurer all funds derived from subscriptions, advertising, and sales of the Bulletin, Torreya, 75-Volume Index, Memoirs, and Index Cards. His books shall be audited at least once every year by the Auditing Committee, and he shall render a report at the Annual Meeting. He shall have charge of all reserve stocks of publications.

Article X Bibliographer

The Bibliographer shall prepare literature citations for publication by the Club, and have charge of the Index Cards of the Club.

Article XI Historian

The Historian shall have charge of the Archives and past records and proceedings of the Club, and shall perform such other duties concerned with the history of the Club as may be assigned.

Article XII Council

The Council shall consist of the President, the last two ex-Presidents, the Vice-President, the Treasurer, the Corresponding and Recording Secretaries, the Editor, the Associate Editor for Torreya, the Manager of Publications, Chairman of the Field Committee, Chairman of the Local Flora Committee, and twelve elected members, of whom four shall be elected each year for terms of three years. Nine members shall constitute a quorum. Vacancies in unexpired terms shall be filled by the Club by ballot.

The Council shall hold a regular meeting just prior to the Annual Meeting and at other times at the call of the President. It shall prepare annually a Budget for consideration by the Club, shall approve all contracts, shall pass upon all extra-budgetary bills presented for payment, shall pass upon candidates for all elective offices, and shall have the power to accept resignations and appoint committees to facilitate the conduct of its business.

It shall be the duty of the Council to invest the funds of the Club. No transfer of any stock, bond, note, or other evidence of debt standing in the name of the Club or withdrawals from savings banks accounts shall be made except by the Treasurer, having the written order of the Council for that purpose, and all such orders shall be countersigned by the President and one of the Secretaries.

Article XIII Members

The membership of the Club shall consist of active (including sustaining and life) and associate members. Associate members may attend all meetings and field trips of the Club, but shall not be eligible to vote or hold office. Each associate member shall receive the notices of the field trips and other announcements of the Club. Each active member shall receive all current publications of the Club except the Index Cards, Memoirs, and other special publications of the Club. Payment at one time of a sum designated by the Council shall entitle a member to become a life member without further payment of dues. After payment of annual dues for forty years, an active member shall be eligible to election to life membership and, in special cases, others may likewise be elected to life membership.

ARTICLE XIV DUES

The dues of all classes of membership shall be fixed by the Council.

ARTICLE XV ELECTION OF MEMBERS

Applications for election to membership shall be voted upon at the next regular meeting of the Club. All memberships shall begin on the first day of the year in which the member is elected, except that members elected after the first day of October may, if they choose, have their membership begin on the first day of the following year.

ARTICLE XVI RESIGNATION OF MEMBERS

A member may at any time resign from the Club on giving notice to the Recording or Corresponding Secretary and paying such sums as he may owe to the Club.

ARTICLE XVII DELINQUENT MEMBERS

Any member who, after due notice, shall for the space of three months neglect to pay his annual dues, shall cease to enjoy the privileges of the Club's membership until they are paid. Any member delinquent for two years shall be dropped from the rolls of the Club unless special arrangements are made with the Treasurer and approved by the Council.

ARTICLE XVIII FISCAL YEAR

The fiscal year shall commence on the first day of January, and all annual dues shall be payable at that time.

ARTICLE XIX ANNUAL MEETING

The first regular meeting in January shall be the Annual Meeting. Fifteen members shall constitute a quorum for the transaction of business.

ARTICLE XX DELEGATES AND REPRESENTATIVES

Delegates and Representatives on the Councils of the New York Academy of Sciences and the American Association for the Advancement of Science, and other organizations with which the Club is or shall become affiliated, shall be elected at the same time and in the same manner as the officers of the Club, the number of such delegates and representatives to be elected depending on the quota regulations of such organizations.

ARTICLE XXI AMENDMENTS

Amendments to this Constitution must be referred to the Council, which shall report thereon at the next regular or special meeting; and at the next regular or special meeting thereafter ensuing (special notice having been given by the Corresponding Secretary) a vote by ballot shall take place on the proposed amendment, and, if the same be approved by three-fourths of the members present, it shall thereafter form a part of this Constitution.

BY-LAWS

1. TIME AND MODE OF ELECTION

A Nominating Committee, appointed by the President, shall select a slate of candidates to consist of officers, Council members, delegates, and representatives, subject to the approval of the Council. This slate will be presented to the Club at a regular meeting, where any active member of the Club may make nominations from the floor. All nominees shall be consulted by the Nominating Committee as to their availability for office. The Nominating Committee shall conduct the election, which shall be by written ballot sent to all active members. Results of the election shall be announced by the Cor-

responding Secretary at the Annual Meeting. All officers shall enter upon the duties of their respective offices immediately after the close of the Annual Meeting.

2. Meetings

Unless otherwise determined by the Club, the regular meetings shall be held on the first Tuesday and third Wednesday of each month from October to May, inclusive, at such time and place as the Club may direct. Nine members shall constitute a quorum for the transaction of business. The President may call special meetings upon his own motion.

3. Order of Business

The following shall be the order of regular business at all meetings of the Club except at the Annual Meeting:

1. Reading of the minutes of the last meeting.
2. Election of new members and announcement of resignations.
3. Reports of committees.
4. Deferred business.
5. New business.
6. Scientific program.

At the Annual Meeting the order of business shall be as follows:

1. Reading of the minutes of the last meeting.
2. Election of new members and announcement of resignations.
3. Reports of officers, delegates, and representatives.
4. Reports of standing committees.
5. Reports of other committees.
6. Deferred business.
7. New business.
8. Report on results of election of officers.

4. Standing Committees

The Standing Committees shall be as follows:

1. Program Committee.
2. Field Committee.
3. Local Flora Committee.
4. Publications Exchange Committee.

5. Program Committee

The Program Committee shall arrange for the scientific program of the meetings of the Club during the year.

6. Field Committee

The Field Committee shall select the dates, places, and leaders of the field trips and publish notices of the same, and may arrange for special indoor meetings for the study of plant material collected.

7. Local Flora Committee

The Local Flora Committee shall consist of two distinct subcommittees, one for the phanerograms and one for the cryptograms, whose duty it shall be to prepare complete and accurate lists of all the plants, native, naturalized, and adventive, occurring within one hundred miles of New York City, and to have such lists published with as much description and illustration as they shall deem best, and as the funds obtainable for that purpose shall warrant. It may arrange for special indoor meetings for the purpose of critically studying plant material assembled for this purpose.

8. Publications Exchange Committee

The Publications Exchange Committee shall consider and, subject to approval by the

Council, pass upon all requests for exchanges of publications with the Club, keep an accurate record of the exchanges, and render a report of the same to the Club at the Annual Meeting.

9. DONATIONS AND BEQUESTS

A record shall be kept by the Treasurer of the source, nature, and description of each donation and bequest.

10. AMENDMENTS TO THE BY-LAWS

Amendments to the By-laws shall be prepared in writing and referred to the Council, which shall report on them at a subsequent regular meeting of the Club, and may be adopted by a majority vote of those present.

An Annotated Preliminary Catalogue of the Vascular Flora of Rockland County, New York

(Continued from Bull. Torrey Club **84**: 48–56, Jan.–Feb., 1957.)

J. HARRY LEHR

SAURURACEAE

SAURURUS

SAURURUS CERNUUS L. Lizard's Tail. Clarkestown, Orangetown. (H)

SALICACEAE

SALIX

*SALIX BABYLONICA L. Weeping Willow. Stony Point. Naturalized along the banks of Minnisceongo Creek.
S. DISCOLOR Muhl. Pussy-willow. General. (H)
S. NIGRA Marsh. Black Willow. Ramapo. (H)
*S. SERICEA Marsh. Silky Willow. Ramapo. (H)

POPULUS

*POPULUS DELTOIDES Marsh. Eastern Cottonwood. Orangetown. (H)
P. GRANDIDENTATA Michx. Bigtooth Aspen. General. (H)
P. TREMULOIDES Michx. Quaking Aspen. General. (H)

MYRICACEAE

MYRICA

MYRICA PENSYLVANICA Loisel. Northern Bayberry. Ramapo, Orangetown. (H)

COMPTONIA

COMPTONIA PEREGRINA (L.) Coult. Sweet-fern. Ramapo, Haverstraw. (H)

JUGLANDACEAE

JUGLANS

*JUGLANS NIGRA L. Black Walnut. Ramapo.

CARYA

CARYA GLABRA (Mill.) Sweet. Pignut Hickory. Ramapo.
C. OVATA (Mill.) K. Koch. Shagbark Hickory. Ramapo. (H)

CORYLACEAE

CORYLUS

CORYLUS AMERICANA Walt. American Hazelnut. Ramapo, Clarkestown, Orangetown. (H)

CARPINUS

CARPINUS CAROLINIANA Walt. var. VIRGINIANA (Marsh.) Fern. American Hornbeam. Ramapo. (H)

BETULA

BETULA LENTA L. Sweet Birch. Ramapo, Orangetown. (H)
B. LUTEA Michx. var. MACROLEPIS Fern. Yellow Birch. Haverstraw. (H)
B. POPULIFOLIA Marsh. Gray Birch. General.

ALNUS

ALNUS RUGOSA (Du Roi) Spreng. Speckled Alder. Stony Point. (H)

FAGACEAE

FAGUS

FAGUS GRANDIFOLIA Ehrh. American Beech. General. (H)
F. GRANDIFOLIA Ehrh. forma PUBESCENS Fern. & Rehd. Ramapo. (H)

CASTANEA

CASTANEA DENTATA (Marsh.) Borkh. American Chestnut. Usually a stump sprout only, but occasionally a small tree. General. (H)

QUERCUS

QUERCUS ALBA L. White Oak. General. (H)
*Q. COCCINEA Muench. Scarlet Oak. General. (H)
*Q. ILICIFOLIA Wang. Bear Oak. Haverstraw. (H)
Q. PRINUS L. Chestnut Oak. General. (H)
Q. RUBRA L. Northern Red Oak. General. (H).
Q. VELUTINA Lam. Black Oak. General. (H)

ULMACEAE

ULMUS

ULMUS AMERICANA L. American Elm. General. (H)
U. RUBRA Muhl. Slippery Elm. Haverstraw.

CELTIS

CELTIS OCCIDENTALIS L. Hackberry. Clarkstown, Stony Point. (H)

MORACEAE

MORUS

*MORUS ALBA L. White Mulberry. Orangetown.

MACLURA

*MACLURA POMIFERA (Raf.) Schneid. Stony Point.

CANNABINACEAE

HUMULUS

HUMULUS JAPONICUS Sieb. & Zucc. Japanese Hops. Haverstraw, Ramapo. (H)
*H. LUPULUS L. Common Hops. Ramapo. (H)

URTICACEAE

LAPORTEA

LAPORTEA CANADENSIS (L.) Wedd. Wood-nettle. Ramapo. (H)

Pilea

Pilea pumila (L.) Gray. Clearweed. Ramapo. (H)

Boehmeria

Boehmeria cylindrica (L.) Sw. False Nettle. Ramapo. (H)

SANTALACEAE

Comandra

Comandra umbellata (L.) Nutt. Bastard Toadflax. Ramapo. (H)

ARISTOLOCHIACEAE

Asarum

Asarum canadense L. Wild Ginger. Ramapo, Clarkestown. (H)

POLYGONACEAE

Rumex

Rumex acetosella L. Sheep-Sorrel. General.
R. crispus L. Curly Dock. General.
R. mexicanus Meisn. Pale Dock. Stony Point.

Tovara

Tovara virginiana (L.) Raf. Jumpseed. General. (H)

Polygonum

Polygonum arifolium L. Halberd-leaved Tear Thumb. Clarkestown.
P. aviculare L. Knotweed. General. (H)
P. cristatum Engelm. & Gray. False Buckwheat. Orangetown.
P. cuspidatum Sieb. & Zucc. Japanese Knotweed. Ramapo. (H)
P. Hydropiper L. Smartweed. Ramapo. (H)
P. hydropiperoides Michx. Mild Water-Pepper. Haverstraw.
P. pennsylvanicum L. var. laevigatum Fern. Pennsylvania Smart-weed. Ramapo.
P. Persicaria L. Lady's-Thumb. General.
P. punctatum Ell. Dotted Smartweed. Ramapo.
P. punctatum Ell. var. leptostachyum (Meisn.) Small. Ramapo.
P. sagittatum L. Arrow-leaved Tear Thumb. Clarkestown.
P. scandens L. Hedge Bindweed. Orangetown.
*P. tenue Michx. Slender Knotweed. Ramapo. (H)

CHENOPODIACEAE

Chenopodium

Chenopodium album L. Lamb's Quarters. General. (H)
C. ambrosioides L. Wormseed. Orangetown. (H)

Atriplex

Atriplex patula L. var. hastata (L.) Gray. Halberd-leaved Orache. Orangetown. (H)

AMARANTHACEAE

Amaranthus

Amaranthus retroflexus L. Amaranth Pigweed. General. (H)

Acnida

Acnida cannabina L. Water-Hemp. Orangetown, Stony Point. (H)

PHYTOLACCACEAE

Phytolacca

Phytolacca americana L. Pokeweed. General. (H)

AIZOACEAE

Mollugo

Mollugo verticillata L. Carpetweed. Ramapo. (H)

PORTULACACEAE

Portulaca

Portulaca oleracea L. Purslane. General.

Claytonia

Claytonia virginica L. Spring-Beauty. Orangetown, Clarkestown, Ramapo. (H)

CARYOPHYLLACEAE

Scleranthus

*Scleranthus annuus L. Knawel. Orangetown. (H)

Paronychia

Paronychia canadensis (L.) Wood. Slender Forked Chickweed. Haverstraw, Ramapo, Clarkestown. (H)

P. fastigiata (Raf.) Fern. Forked Chickweed. Ramapo. A single station at one of its northernmost points of distribution in New York State. (H)

Arenaria

*Arenaria lateriflora L. Grove-Sandwort. Ramapo, Clarkestown. (H)

Stellaria

Stellaria graminea L. Grass-leaved Stitchwort. Ramapo, Clarkestown. (H)

S. media (L.) Cyrillo. Chickweed. General.

Cerastium

Cerastium arvense L. Field Chickweed. Clarkestown. (H)

C. vulgatum L. Mouse-ear Chickweed. Ramapo. (H)

Lychnis

Lychnis alba Mill. White Campion. Orangetown. (H)

Silene

S. antirrhina L. Sleepy Catchfly. Orangetown. (H)

*S. armeria L. None-so-Pretty. Ramapo. Occuring as a rare escape rather than as a weed. (H)

*S. caroliniana Walt. var. pennsylvanica (Michx.) Fern. Wild Pink. Orangetown. (H)

S. Cucubalus Wibel. Bladder-Campion. Ramapo, Clarkestown.

Dianthus

Dianthus armeria L. Deptford Pink. General. (H)

NYMPHAEACEAE

Nuphar

Nuphar advena (Ait.) Ait f. Yellow Pond-Lily. Clarkestown.

NYMPHAEA

NYMPHAEA ODORATA Ait. Fragrant Water-Lily. Ramapo.

RANUNCULACEAE

RANUNCULUS

RANUNCULUS ABORTIVUS L. Small-flowered Buttercup. Ramapo, Clarkestown, Orangetown. (H)
R. ACRIS L. Tall Field Buttercup. General. (H)
R. BULBOSA L. Bulbous Crowfoot. Clarkestown, Stony Point. (H)
R. FASCICULARIS Muhl. Early Buttercup. Clarkestown.
R. RECURVATUS Poir. Rough Crowfoot. Clarkestown, Stony Point. (H)
R. SCELERATUS L. Cursed Crowfoot. Ramapo. (H)
R. SEPTENTRIONALIS Poir. Swamp Buttercup. Ramapo.

THALICTRUM

THALICTRUM DIOICUM L. Early Meadow-Rue. Clarkestown, Ramapo.
T. POLYGAMUM Muhl. Tall Meadow-Rue. Clarkestown, Ramapo.

ANEMONELLA

ANEMONELLA THALICTROIDES (L.) Spach. Rue-Anemone. Ramapo, Clarkestown, Orangetown. (H)

HEPATICA

HEPATICA AMERICANA (DC.) Ker. Hepatica. Ramapo, Clarkestown, Orangetown. (H)
H. AMERICANA (DC.) Ker., forma CANDIDA Fern. Clarkestown, Orangetown, Ramapo. (H)

CLEMATIS

CLEMATIS VIRGINIANA L. Virgin's-Bower. Ramapo, Clarkestown. (H)

CALTHA

CALTHA PALUSTRIS L. Marsh-Marigold. Ramapo, Clarkestown. (H)

TROLLIUS

TROLLIUS LAXUS Salisb. Globe-Flower. Ramapo. A single thriving station for this rarity. (H)

AQUILEGIA

AQUILEGIA CANADENSIS L. Wild Columbine. General. (H)

ACONITUM

*ACONITUM CARMICHAELII DEBX. Garden Monkshood. Clarkstown. (H)

CIMICIFUGA

CIMICIFUGA RACEMOSA (L.) Nutt. Black Snakeroot. Haverstraw, Stony Point. (H)

ACTAEA

ACTAEA PACHYPODA Ell. White Baneberry. General. (H)

BERBERIDACEAE

PODOPHYLLUM

*PODOPHYLLUM PELTATUM L. May-Apple. Ramapo, Haverstraw. (H)

CAULOPHYLLUM

*CAULOPHYLLUM THALICTROIDES (L.) Michx. Blue Cohosh. Ramapo. (H)

MENISPERMACEAE

Menispermum

Menispermum canadense L. Moonseed. Haverstraw. (H)

MAGNOLIACEAE

Liriodendron

Liriodendron tulipifera L. Yellow-Poplar. General. (H)

LAURACEAE

Sassafras

Sassafras albidum (Nutt.) Nee. Sassafras. General. (H)

Lindera

Lindera Benzoin (L.) Blume. Spicebush. General. (H)

PAPAVERACEAE

Sanguinaria

Sanguinaria canadensis L. Bloodroot. Clarkestown, Ramapo. (H)

Chelidonium

Chelidonium majus L. Celandine. Ramapo, Clarkestown. (H)

Adlumia

Adlumia fungosa (Ait.) Greene. Climbing Fumitory. Stony Point, Clarkestown. (H)

Dicentra

Dicentra Cucullaria (L.) Bernh. Dutchman's-Breeches. Clarkestown. (H)

Corydalis

Corydalis flavula (Raf.) DC. Yellow-Corydalis. Clarkestown. (H)
C. sempervirens (L.) Pers. Pale Corydalis. Haverstraw. (H)

CRUCIFERAE

Berteroa

*Berteroa incana (L.) DC. Hoary Alyssum. Ramapo. (H)

Lepidium

Lepidium campestre (L.) R. Br. Field Peppergrass. Stony Point, Ramapo.
L. virginicum L. Peppergrass. Ramapo.

Capsella

Capsella Bursa-pastoris (L.) Medic. Shepherd's-Purse. General. (H)

Alliaria

*Alliaria officinalis Andrs. Garlic-Mustard. Haverstraw.

Sisymbrium

*Sisymbrium altissimum L. Tumble-Mustard. Ramapo. (H)

Arabidopsis

*Arabidopsis Thaliana (L.) Heynh. Mouse-Ear-Cress. Stony Point. (H)

HESPERIS

HESPERIS MATRIONALIS L. Mother-of-the-Evening. Ramapo, Clarkestown. (H)

BUNIAS

*BUNIAS ORIENTALIS L. A single station for a rare adventive from Eurasia. Fully established and spreading in this area. Clarkestown. (H)

RORIPPA

RORIPPA ISLANDICA (Oeder) Borbas. Marsh Cress. Clarkestown. (H)

NASTURTIUM

NASTURTIUM OFFICINALE R. Br. Watercress. Ramapo.

ARMORACIA

*ARMORACIA LAPATHIFOLIA Gilib. Horseradish. Clarkestown, Stony Point.

BARBAREA

BARBAREA VULGARIS R. Br. Winter Cress. General. (H)

DENTARIA

DENTARIA DIPHYLLA Michx. Toothwort. Clarkestown, Orangetown. (H)
D. LACINIATA Muhl. Cut-leaved Toothwort. Stony Point. (H)

CARDAMINE

CARDAMINE BULBOSA (Schreb.) BSP. Spring Cress. Ramapo. (H)
*C. PARVIFLORA L. var. ARENICOLA (Britt.) O. E. Schulz. Small-flowered Bitter Cress. Haverstraw, Clarkestown. (H)
*C. PENSYLVANICA Muhl. Pennsylvania Bitter Cress. Ramapo. (H)

ARABIS

*ARABIS CANADENSIS L. Sicklepod. Clarkestown. (H)
A. LAEVIGATA (Muhl.) Poir. Smooth Rock Cress. Clarkestown. (H)

RESEDACEAE

RESEDA

*RESEDA LUTEA L. Yellow Cut-leaved Mignonette. Stony Point. (H)

SARRACENIACEAE

SARRACENIA

*SARRACENIA PURPUREA L. Pitcher-Plant. Haverstraw. Found only in the Ramapo Mountain bogs at an altitude above 1100 feet. (H)

DROSERACEAE

DROSERA

*DROSERA ROTUNDIFOLIA L. Round-leaved Sundew. Ramapo, Clarkestown. Found only in the Ramapo Mountains at an altitude exceeding 1100 feet. (H)

CRASSULACEAE

SEDUM

SEDUM ACRE L. Mossy Stonecrop. Stony Point, Ramapo. (H)
S. PURPUREUM (L.) Link. Live-Forever. Ramapo.

SAXIFRAGACEAE

Penthorum

Penthorum sedoides L. Ditch-Stone-crop. Ramapo. (H)

Saxifraga

Saxifraga pensylvanica L. Swamp-Saxifrage. Ramapo. (H)
S. virginiensis Michx. Early Saxifrage. Clarkestown, Stony Point. (H)

Heuchera

Heuchera americana L. Alumroot. Clarkestown. (H)

Mitella

Mitella diphylla L. Mitrewort. Ramapo, Haverstraw. (H)

Chrysosplenium

Chrysosplenium americanum Schwein. Golden Saxifrage. (H)

Parnassia

*Parnassia glauca Raf. Grass-of-Parnassus. Ramapo. A single station which has been destroyed since its first report. (H)

Ribes

Ribes sativum Syme. Red Currant. Ramapo.

HAMAMELIDACEAE

Hamamelis

Hamamelis virginiana L. Witch-Hazel. General.

Liquidambar

Liquidambar Styraciflua L. Sweetgum. Stony Point.

PLATANACEAE

Platanus

Platanus occidentalis L. American Sycamore. Stony Point.

ROSACEAE

Physocarpus

Physocarpus opulifolius (L.) Maxim. Ninebark. Haverstraw.

Spiraea

Spiraea latifolia (Ait.) Borkh. Meadow-Sweet. General. (H)
S. tomentosa L. Steeplebush. General. (H)

Sorbaria

*Sorbaria sorbifolia (L.) A. Br. False Spiraea. Ramapo. (H)

Pyrus

Pyrus arbutifolia (L.) L. f. Red Chokeberry. Haverstraw.
*P. floribunda Lindl. Purple Chokeberry. Clarkestown.
P. Malus L. Apple. General. Commonly spread from or remaining after cultivation. Apple production is an important part of this county's agriculture.
*P. melanocarpa (Michx.) Willd. Black Chokeberry. Clarkestown. (H)

AMELANCHIER

AMELANCHIER CANADENSIS (L.) Medic Serviceberry. Haverstraw, Clarkestown, Ramapo. (H)

CRATAEGUS

CRATAEGUS SSP. The author has not completed his collections and study of this difficult taxon.

FRAGARIA

FRAGARIA VIRGINIANA Duchesne. Wild Strawberry. General. (H)

POTENTILLA

POTENTILLA ARGENTEA L. Silvery Cinquefoil. Clarkestown. (H)
P. ARGUTA Pursh. Tall Cinquefoil. Clarkestown. (H)
P. CANADENSIS L. Cinquefoil. General. (H)
P. NORVEGICA L. Rough Cinquefoil. Ramapo. (H)
P. RECTA L. Sulphur Cinquefoil. Ramapo. (H)

GEUM

GEUM CANADENSE Jacq. Avens. Ramapo.
G. RIVALE L. Purple Avens. Ramapo. (H)

RUBUS

RUBUS ODORATUS L. Purple-Flowering Raspberry. General. (H)
R. PHOENICOLASIUS Maxim. Wineberry. Haverstraw. (H)
R. ssp. The author has not completed his collections and study of other species in this difficult taxon.

AGRIMONIA

AGRIMONIA GRYPOSEPALA Wallr. Agrimony. Ramapo. (H)
A. PARVIFLORA Ait. Many-flowered Agrimony. Ramapo, Orangetown.

ROSA

ROSA CAROLINA L. Low Pasture Rose. Clarkestown.
*R. MULTIFLORA Thunb. Rambling Rose. Ramapo, Clarkestown.
*R. PALUSTRIS Marsh. Swamp Rose. Clarkestown.

PRUNUS

PRUNUS PENSYLVANICA L.f. Pin Cherry. Ramapo, Clarkestown. (H)
P. PERSICARIA (L.) Batsch. Peach. General. (H)
P. SEROTINA Ehrh. Black Cherry. General. (H)

(to be continued)

FIELD TRIP REPORTS

June 22–23, 1956. St. Johnsbury, Vermont. This outing was with the Vermont Botanical and Bird Club. There were fifteen Torrey Club members on hand. The most exciting species were *Calypso bulbosa, Saxifraga aizoides,* and *S. oppositifolia.* There were many ferns, orchids, and other showy plants. The northern affinity of this upper Connecticut River region was brought out also by such plants as *Clintonia borealis, Primula Mistassinica, Draba lanceolata, Corallorhiza trifida* var. *verna,* and *Kalmia polifolia.* People who have looked in vain for the *Cyprepedium parviflorum* station reported in New Jersey were able to see the plant on this trip. Leader, James Marvin.

Sept. 23. Van Cortlandt Park, N. Y. There was little bird activity and the afternoon was spent observing trees, shrubs, and wild flowers. We looked for ironwood which

used to grow in abundance in the swamp or along the margin but was not seen on this walk along the Swampside Trail. Attendance 3. Leader, Jane Meyer.

Nov. 3. Long Branch to Toms River, N. J. The autumn water-fowl trip encountered weather little better than that reported for the spring visit. Twenty-seven species of birds were recorded, more than half of them waterfowl. The rest were permanent residents or winter residents such as the chickadee and junco. The study of Mr. Wisner's collection of birds' nests at his home in West Long Branch was well worth the effort of the whole trip. Attendance 11. Leader, Barbara Cook.

Nov. 4. Hutcheson Memorial Forest, East Millstone, N. J. The autumnal aspect of this mature oak forest was examined. Leaf fall was completed except for the persistent leaves of some oaks and beech that will hang on most of the winter, though brown and dead. Winter greens such as Allium, Japanese honeysuckle, Geum, Heuchera, aborted buttercup, and yellow rocket were conspicuous. One member of the group found the first leaves of spring beauty. Mosses were obvious but ferns had disappeared, above the ground at least. Some winter fruiting fungi were studied. Another interesting aspect of the woods was the occurrence and distribution of fruits. Under hickories, oaks, or beech, the fruits were rarely encountered. Dogwood, fruits, on the other hand were abundant both on trees and on the litter of the forest floor. Apparently they appeal less to the woodland fauna. The black and wrinkling fruits of maple-leaved viburnum were abundant on this most frequent plant of the upland shrub layer. Arrow-wood and spicebush, shrubs of the lowland, had passed the time for profitable study of their fruits though an occasional one was found. A search of the swamp for skunk cabbage turned up buds only though flowers have been recorded later in the month some seasons. Attendance 21. Leaders, Murray F. Buell and Carl Monk.

Proceedings of the Club

MAY 15, 1956 The meeting was called to order by President Barton at Columbia University, at 8:03 P.M. Thirty-nine persons were present. The Minutes of the meeting of May 1, 1956 were approved as read.

Two new members were elected to active (annual) membership by the Club; Miss Ernesta J. Forlano and Dr. Hugh H. Iltis. One associate member, Miss Sadie Yass, was also elected. The resignation of Mr. Franc Ritter was accepted with regret.

President Barton introduced the speaker of the evening, Dr. Phillip Woods of the Brookhaven National Laboratories who gave an illustrated talk on, "The Effects of Antimetabolites on Cell Division". A question and answer period followed the talk. Dr. Woods' abstract follows:

Effects of Certain Antimetabolites on Mitosis

Onion roots were grown for various periods of time on solutions of substances believed to inhibit nucleic acid synthesis. After fixation in 3:1 alcohol acetic and staining in Feulgen reagent, root-tips were studied cytologically.

Both benzimidazole and 5-aminouracil, analogues of purines and pyrimidines respectively, caused a reduction in number of division figures in treated roots. A sudden decline occurred at the beginning of treatment with benzimidazole (300 micrograms per ml.) but not until 6 or more hours later with 5-aminouracil (100 micrograms per ml.)

After 24 hours of treatment with 5-aminouracil, small interstitial portions of metaphase chromosomes were observed to be Feulgen-negative and these regions were extended into thin strands during anaphase. Since micronuclei were rarely observed, breakage apparently does not take place. Stickiness resulting in chromosome bridges was also not observed. Following treatments with benzimidazole the only morphological change appeared to be a slight increase in amount of contraction of metaphase and anaphase chromosomes. No Feulgen-negative regions appeared. Neither of the analogues affected the spindle mechanism at these concentrations.

On the assumption that the analogues would interfere with nucleic acid synthesis, estimations of DNA content of nuclei were obtained by measuring the amount of Feulgen-dye per nucleus with a microphotometer. In control roots two classes of interphase

nuclei occurred; the nuclei of one class contained twice as much DNA (Feulgen stain) as the other and the two types occurred at about equal frequency. Prophase nuclei always contained the doubled amount of DNA and telophases the reduced amount. DNA synthesis apparently occurs during a brief period at the mid-point of interphase. Roots treated with 5-aminouracil for 24 hours contained few nuclei of the class with the greater amount of DNA (Feulgen stain). Apparently 5-aminouracil affects only one step in the mitotic cycle, namely the doubling of DNA in interphase whereupon divisions cease. In roots treated with benzimidazole for 24 hours the relative frequency of the two classes of nuclei was not altered; however, mitotic activity was reduced. Such findings would suggest that benzimidazole affects two different steps in the mitotic cycle: 1) processes necessary for the doubling of DNA and 2) processes necessary for the onset of prophase.

The meeting was adjourned at 9:05 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

October 20, 1956. At the end of an afternoon devoted to a tour of the Brooklyn Botanic Garden, and after the serving of refreshments by the Garden's staff, the meeting was called to order at 5:10 P.M. by President Barton; 40 were present. The minutes of the preceding meeting were read and approved.

James H. Zimmerman and Elizabeth Harrold were elected to active membership, and Amy von der Porten, Bonnie B. Wilkinson, and John M. Price to associate membership.

The matter of microcards of out-of-print volumes (1–23) of the Bulletin was discussed, as was the project to secure the Tannersville bog as a nature preserve. Plans were announced for the meeting and exhibits sponsored by the Club in connection with the coming meeting of the A.A.A.S. It was announced that the Council had increased the dues for Active Members to $7.50 beginning with 1957.

On behalf of the Committee (J. A. L. Simpson, H. D. Rickett, D. P. Rogers) for the Revision of the Constitution and By-Laws, the last named proposed the adoption of a number of alterations, and presented the objectives of each.

Certain members who had come provided with lantern slides then reported on their summer experiences: Miss Gertrude Phillips, in Alaska; Dr. Elva Lawton, research and travel in the Northwest; Dr. Paul Burkholder, the Brooklyn Botanic Garden's new field station in Westchester County; Mr. Winthrop Means, flowers of Mt. Ranier and Mt. Hood; Dr. Marion Johnson, in Puerto Rico.

The Club voted to express its appreciation for the entertainment provided by the Brooklyn Botanic Garden after which the meeting was adjourned at 6:30 P.M.

Respectfully submitted
Donald P. Rogers
Recording Secretary
pro tem

November 20. The meeting, at Columbia University, was called to order by President Barton at 8 P.M.; 62 were present. The minutes of the preceding meeting were read and approved.

Mr. Edwin L. Thompson was elected to active (annual) membership by the Club.

Dr. Rickett of the Committee to Revise the Constitution and By-Laws read the proposed changes to the Constitution and By-Laws as required by the Constitution:

The scientific portion of the program consisted of a talk by Dr. Paul R. Burkholder of the Brooklyn Botanic Garden on, "Studies in Marine Microbiology".

These studies were concerned with the activity of bacteria found in the mud of *Spartina* marshes along the south Atlantic Coast. The role of these bacteria in the formation of cobalamin, Vitamin B_{12}, was discussed. Marine bacteria of the genus *Pseudomonas*, were among the organisms involved in the process. One of the parts played by these organisms is the possible transformation of low value proteins to high value proteins. Recent work on the marine bacteria of Long Island Sound was also discussed.

The talk was followed by a question and answer period after which the meeting was adjourned at 9:10 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

December 4. The meeting, at Columbia University, was called to order by Vice-President Moul at 8 P.M.; 33 were present.

The minutes of the previous meeting were approved as read.

Dr. Moul read a letter sent by Dr. William Stern of the Yale School of Forestry concerning the rise in dues, changes to the Constitution, the sending of notices to the meetings, and other problems. It was suggested that these problems be considered by the Council at its next meeting.

Voting, by the active members, on the proposed changes to the Constitution was the next order of business. Nineteen active members were present. Three-quarters of these or 14 votes were required for the approval of the changes.

Dr. M. A. Johnson moved that the changes be taken up article by article. This motion was seconded and approved by the members.

Changes to Article III Officers, were considered first. After the reading of the proposed changes by Dr. Rickett, Mr. Fairbrothers introduced an amendment to the proposed changes which stated that the President could not be re-elected to office until after one year had elapsed. The vote on the amendment was 8 for and 6 against. Since this was not a ¾ majority the amendment did not pass. The vote on the original proposed changes was 10 for and 6 against, also not a passing vote.

Since the changes to Article III were not accepted, the changes to Article V were not voted upon since they depended upon the passing of the changes in Article III.

The changes to Article VI were passed with a favorable vote of 15.

The part of the changes to Article VII which stated "after 'Council' insert 'received all applications for membership'" was passed with a favorable vote of 14; the other parts were not voted upon since they hinged on the passing of the changes to Article III.

The change to Article VIII was accepted with a favorable vote of 16.

The changes to Article IX concerning the duties of the Business Manager were accepted by a favorable vote of 19.

It was then suggested that the changes to Article III be reconsidered since only one of these changes, the one dealing with the re-election of officers, was unacceptable.

The change eliminating the Second Vice-President from the officers was accepted by a favorable vote of 15; the change of the title of the Business Manager to Manager of Publications was accepted by a favorable vote of 17; the addition of an Historian to the officers was accepted by a favorable vote of 18.

The changes in Article XI Council, were accepted by a vote of 17 for the change.

The change dealing with Article XIV Election of Members, was accepted by a vote of 19 for the change.

The change in Article XX Amendments, was favorably accepted by a vote of 18.

The change to By-Law 1 was accepted by a positive vote of 17.

The changes to Article VII, Secretaries, pertaining to the duties of the Corresponding Secretary, the addition of a new Article XI outlining the duties of the Historian, and a provision for renumbering following articles were all accepted by a favorable vote of 16.

Dr. Rickett then moved that all the accepted changes should become effective immediately. This motion was seconded and passed by a vote of 19.

Dr. Moul then introduced the speaker of the evening, Dr. John J. Mayernik of Merck and Company, who addressed the Club on, "Trouble Spots in the Microbiological Assay of Vitamin B_{12}". After the talk there was a lively discussion period which brought the meeting to a close.

The meeting was adjourned at 9:30 P.M.

Respectfully submitted
Frank G. Lier
Recording Secretary

[The changes in phrases of the Constitution and By-Laws have been omitted. They are in the Secretary's Minutes. They have been circulated to members. The revised Constitution is printed above.—ED.]

BOOK REVIEWS

Grasslands of the Great Plains: Their Nature and Use. By J. E. Weaver and F. W. Albertson. Johnsen Publishing Co., Lincoln, Nebraska. ix + 395 pp. 93 figs. 1956.

This book deals with the "mixed prairie" (*Stipa-Bouteloua* Association), which occupies the portion of the Great Plains between about the hundredth meridian and the Rocky Mountains. It is a companion volume to Weaver's recent book[1] on the "true prairie" (*Stipa-Sporobolus* Association). The mixed prairie is the largest unit of the grassland formation in North America stretching from southern Canada, (about 53°N) to southern Texas (30°N). The history of this great grassland area is discussed in relation to the effect of natural environmental factors upon its development and in connection with the modifications which were brought about by settlement. The botanical composition of the vegetation is discussed in relation to the ecologcal factors, including grazing, which determine the various communities which comprise it. In addition, a story is told about each of the principal dominant and sub-dominant species of the area. All of this is developed upon an ecological background in a way that makes the reader appreciate how the forces of nature have interacted to produce this interesting flora. The form of presentation is such as to appeal to both the botanist and the less technical reader.

Perhaps the most outstanding part of the work is concerned with the effects of drought during the 1930's upon this vegetation, the recovery of the vegetation from drought during a decade of relatively favorable weather, and a record of the onset of drought again in the early 1950's. This classical record has been condensed from the extensive papers by the authors, which have been made possible only because of their untiring efforts to secure a lasting account of the responses of the vegetation to changes in weather patterns. It is based on critical examination of numerous prairie areas in western Kansas and Nebraska and in parts of Oklahoma, Colorado, Wyoming and South Dakota for the last 25 years. Their studies are representative, since they were conducted in the central part of the mixed prairie. Reports of less extensive studies of the effect of drought in other mixed prairie areas are included by means of a thorough review of the literature.

In order to make the book applicable to the whole region of the mixed prairie, the authors have gone to considerable trouble to have portions of the book written or criticized by persons in other parts who are familiar with the local vegetation. Consequently, special chapters are included on the mixed prairie vegetation of Colorado, Oklahoma, Texas, New Mexico, Montana, Wyoming, North Dakota, South Dakota and southern Canada. This volume, together with Weaver's previous book, must now be considered as the most reliable and extensive reference on the grasslands of the Great Plains and Central Prairie of North America. A similar work is not available for the grasslands of any other part of the world. This book should therefore be an inspiration to those who are conducting such studies elsewhere. It is fortunate that this work has been conducted at a time when some relatively undisturbed grassland sites still occur in the Great Plains.—R. T. COUPLAND, Department of Plant Ecology, University of Saskatchewan, Saskatoon, Sask., Canada.

[1] Weaver, J. E. 1954. North American Prairie. Johnsen Publishing Co., Lincoln, Nebraska, xii + 348 pp. 87 figs.

A Comparative Study of Chlorococcum meneghini and Other Spherical, Zoospore-Producing Genera of the Chlorococcales. Indiana University Publication. Science Series #20. Indiana University Press, Bloomington. $3.

The taxonomy of the algae in the past has for the most part been based, as in the higher plants, primarily on morphological characters. With the macroscopic forms such as the large marine Chlorophyta, Phaeophyta and Rhodophyta, this has usually been satisfactory. However, among the green algae and some of the other groups, there are many unicells in which because of their smallness, morphological characters are useless. This is true because such characters are few and difficult to observe. Another fact that must be remembered in respect to these unicells is the possibility that many of the taxa described as species on the basis of morphological characters may be only a stage in the life cycle of another species. Recently, this has been shown to be true in a number of cases. Lastly, in respect to the use of morphological characters alone, because of inadequate descriptions in the past it has been shown that one taxon has been described at several different times under different names. This has led to a confused taxonomic situation involving a staggering array of synonyms.

In recent years, with advance culture methods for the algae, it has become possible to isolate individual forms and grow them in unialgal cultures for a long period of time. In this way not only can the morphology of the phase isolated be studied, but also the morphological changes that occur during the life cycle of the cultured form. The difficulty here lies in the fact that not all of those interested in the algae have the facilities or time to culture every unknown or questionable species; hence, a long period of years will probably elapse before workers have followed this procedure with all the algae and made the information available for those working in the field of Phycology.

Dr. Richard C. Starr has given us in this paper an excellent comparative study of one of the most controversial groups in the Chlorophyta. Through the study of unialgal cultures of a number of the spherical members of the Chlorococcaceae, he has established the limits of a number of genera in terms of the type of zoospore, the type of chromatophore in the vegetative cell and the presence or absence of a pyrenoid.

The genera, *Chlorococcum*, *Radiosphaera*, *Bracteacoccus*, *Dictyochloris*, *Trebouxia*, *Nantococcus* and *Planktosphaeria* are redescribed and the generic limits defined. New genera, *Spongiochloris* and *Neochloris* are established. Within these genera a number of species are redescribed or new species added. Excellent illustrations are provided to augment the descriptions in the text, giving the stages in the life cycle in all species treated. A key to the spherical, zoospore-producing genera covered by the text is included.

More monographs of this nature will certainly be exceedingly helpful to the taxonomist. It will not enable him to identify everything he finds in natural collections, but will certainly aid in solving some of the puzzling taxonomic problems with which he is faced at present.—E. T. Moul. Dept. of Botany. Rutgers University.

New Concepts in Flowering-Plant Taxonomy. By J. Heslop-Harrison. i-viii, 1–135. *f. 1–10.* Harvard University Press. 1956. $1.25.

This little book appeared first in England in 1953 and is now reprinted in this country (without indication of its previous publication). In spite of its title, its discussion of taxonomy in the light of modern investigation is valid for all living things; the illustrative material is drawn mainly from flowering plants.

During the nineteenth century and for part of the twentieth, the taxonomists played a game of solitaire. Other botanists, as they developed better methods of chemical and microscopic study and established connections with other sciences, did not generally concern themselves with the classification or naming of the plants they studied. If they wrote about evolution, it was mainly to speculate upon the relationships of the larger groups as indicated by morphological researches. But in recent decades, cytologists and geneti-

cists have attacked evolution by studying the relationships of actual plant populations, thus invading the purlieus of the systematist. The impact of this incursion is the subject of this book.

Beginning with a review of the aims and methods of "classical" taxonomy from de Candolle to Darwin and to the present time, Heslop-Harrison takes up such subjects as the statistical treatment of variation, experiments with transplantation, geographical variation, isolating mechanisms internal and external, cytology as related to taxonomy, and the place of hybridization in evolution. One of the outstanding developments of the "new systematics" is the transfer of emphasis from *specimens* to *populations;* this distinction is clearly pointed out on many pages of the book. As the author says, a "rigid species concept based upon the meticulous description of 'type' individuals" has proved inadequate to elucidate many difficult genera. [For the much misused word "meticulous," surely not here intended, see any dictionary.] It is important to point out (as he does not) that the "type method" to which he several times refers is not the "type method" of nomenclature, but the basing of taxonomic judgments upon specimens thought to be "typical." Classical taxonomy was necessarily subjective in its judgments; experimental taxonomy should be much less so. And most of us now realize "the absurdity of the attitude prevalent in the nineteenth century that *all* groups *must* be amenable to treatment by defining and naming 'species' if only taxonomists were competent to detect the real lines of demarcation."

The study of natural populations and especially the use of cytogenetic methods in explaining their variation and propagation have resulted in new categories which have taken their place somewhat confusingly beside the genera, species, subspecies, etc. of the "orthodox" taxonomist. Coenospecies, convivia, parageneons, ecotypes, gamodemes, and numerous other terms denote the sometimes unstable concepts of many experimental workers. One of the most valuable contributions of this book is a clear comparison of the various systems of Turesson, Danser, Clausen, Keck and Hiesey, Gregor, Gilmour, Camp and Gilly, and others. The author points out also (as no other whom I have read does) the difference between categories founded directly on the observation of populations in nature, as the earlier concept of ecotypes, and those based on theoretical standards, as the "inability" to exchange genes (one rarely finds an empiric method of testing "inability"). Some of the modern experimenters, in their anxiety to develop a system, have ventured rather far into such theoretical categories.

Finally, what is the outlook for a study of evolution and a taxonomic discipline using different sets of categories which may be incommensurable? "It is worth noting that this new biological discipline [experimental taxonomy] is perhaps in a way not a form of 'taxonomy' at all since the production of *classifications* is no part of its basic aims." And again, "looking past the present conflict of categories . . . we may perhaps glimpse a future in which the defining of categories has been abandoned altogether . . ." in the study of evolution. I hope that this prognostication is no more reliable than our local weather prophecies, and that taxonomy can keep in tune with evolutionary thought while the study of evolution continues to use taxonomic names for the populations with which it deals. In any case, no knowledge can ever progress without making classifications!

The extraordinarily clear summarizing of so vast a range of subjects in so small a space merits high praise. Of course there are minor incoherencies and inaccuracies; but to mention any would only demonstrate the dyspepsia of the reviewer. Because of the inevitably condensed treatment, the book may be difficult for a student just entering the field. But as a review and guide for more experienced students of plants, especially for the taxonomist, it should be invaluable.—H. W. RICKETT.

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